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A MANUAL OF VETERINARY PHYSIOLOGY

A MANUAL
OF
VETERINARY PHYSIOLOGY

BY

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DEDICATED

TO THE MEMORY OF

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M.A., M.D., LL.D., D.C.L., F.R.S.,

LATE PROFESSOR OF PHYSIOLOGY IN THE
UNIVERSITY OF CAMBRIDGE

PREFACE TO FIFTH EDITION

This book was due for revision in 1914, but the outbreak of War and my recall to military service prevented its being taken in hand; to meet the demand, two small editions were successively reprinted.

As the War continued, it was decided either that the work must remain out of print or the text be brought up to date by another hand. Dr. T. H. Milroy, Professor of Physiology in the Queen's University of Belfast, very kindly undertook the revision of that portion of the book dealing with general physiology. My thanks are due to him for his help rendered at great personal inconvenience in the midst of his own exacting duties. The first five chapters were in the press when my release from Military Service, in the autumn of 1919, rendered it possible for me to undertake revision on a broader basis than was originally intended. Several chapters have accordingly been recast or entirely rewritten.

I have been taken to task for calling this work a Veterinary Physiology, but the title was not chosen without due consideration. It is not a comparative physiology, but a work intended for veterinary students and practitioners. Throughout its pages an attempt has been made to show the bearing of physiology on the practice of veterinary medicine, surgery, and hygiene.*

The chapter on Generation and Development is long, but I make no apology for this; the subject is of extraordinary interest to the veterinarian. The breeding of animals is not hampered by social laws and that neglect of heredity which in human beings leads so largely to the multiplication of the unfit.

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* It is the great regret of my life that with unrivalled facilities for clinically studying two big groups of diseases affecting horses—namely, those of the Digestive and Locomotor systems—I have been able to add so little to the common stock of knowledge. Ignorance of the diseases of animals will remain until those forces capable of overcoming pathological secrets combine to attack the question. The clinician, pathologist, physiologist, biochemist, biologist, and entomologist are all in a greater or less degree concerned; in the future, laboratory team work must play a far larger part if progress is to be made.

The section on breeding has been dealt with by Mr. J. B. Robertson, M.R.C.V.S., whose practical knowledge of the subject is balanced by his scientific interest. I regard myself as exceptionally fortunate to have secured his able co-operation.

We sometimes require to be reminded of the fact that in these islands all the domestic animals have been brought to a state of development unapproached by any other country in the world.* The local conditions, so favourable to the improvement of breeds, have fortunately been supplemented by a special gift of native intelligence.

The all-important study of animal nutrition may be claimed to have been very largely initiated in this country; it was at Rothamsted, at the private expense of the late Sir John Lawes, that researches, extending over twenty years, were carried out, in conjunction with the late Sir Joseph Gilbert, into the economical feeding of animals and the storage of food by the body.† None of the physiological conclusions of these observers, though seventy years old, have been cast aside as out of date. They established the fundamental facts on which the scientific work of Animal Nutrition Stations on the Continent of Europe and in the United States of America has been so largely built. I am especially indebted to the work of Dr. H. P. Armsby, Director of the Institute of Animal Nutrition of the Pennsylvania State College, U.S.A., which I have freely drawn upon in endeavouring to present a summary of the highly complex subject of the means by which the system obtains its nourishment from food, and of what it does with it subsequently.

In a review of the last edition there was a complaint that the physiology of the cell was inadequately dealt with. I fear that I am impenitent; if more information is required, there are numerous works from which it can be obtained. I need all the space I can command for subjects of greater practical importance, some of which are not dealt with elsewhere, and many of which are so scattered through periodicals as to be unavailable, excepting to the research student.

For the same reason the chemical facts have been dealt with

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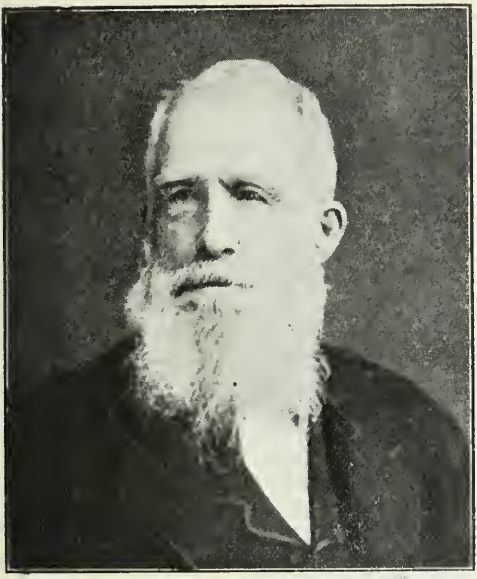
* "Every breed of live-stock with which he was familiar, and which it was the ambition of his countrymen to raise successfully, came originally from Great Britain. It was one of the most remarkable things in human history that practically all the great domestic animals on which mankind relied for sustenance and support had been brought to perfection in Great Britain and distributed throughout the world. If there were nothing else in British history to make it glorious, that alone was a matter for unceasing pride."—Report of speech by H.E. the American Ambassador on "British Stock," *Morning Post*, August 3, 1920.

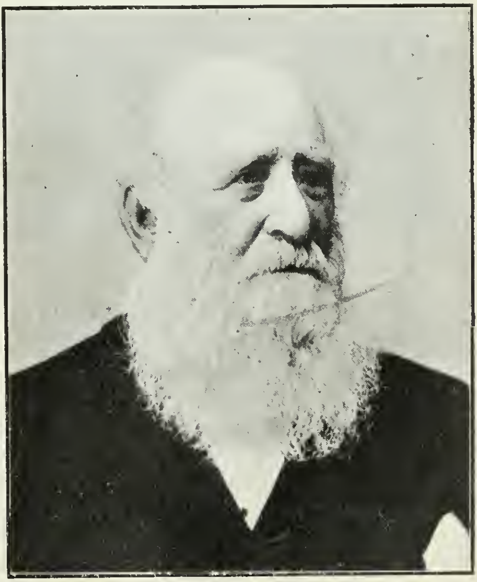
† My thanks are due to Dr. E. J. Russell, F.R.S., the present Director of the Rothamsted Experimental Station, for copies of the photographs of Sir John Lawes and Sir Joseph Gilbert.



SIR JOHN LAWES, F.R.S.

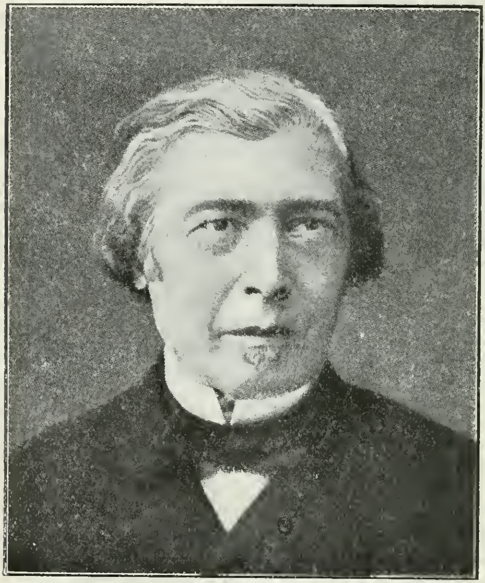
only at sufficient length to elucidate the text, while the concluding chapter on the chemistry of the body, very kindly contributed by Professor Milroy, is intended only as an outline of a subject which has grown far beyond the needs of any other than a student desirous of a University degree, for whom the necessary textbooks are available.

I made a special point in the last edition of drawing the attention of the English reader to the great debt he owes to the labours of the late Professor G. Colin, of the Veterinary School of Paris, as the father of veterinary physiology. Though his work appeared more than fifty years ago, and vast strides have been made since his day, nothing can disturb the accuracy of his experimental work. I am indebted to Mr. A. H. Hunter, M.R.C.V.S., of Le Hâvre, for the trouble he has taken in securing me a copy of a photograph of this great man.



[SIR JOSEPH GILBERT, F.R.S.

I have been favoured with help from many members of the profession whose names appear in the text, and to whom I am indebted for new facts or observations which I no longer have an opportunity of repeating or making. I would mention in this connection the staff of the Army Veterinary School, Aldershot, where, through the co-operation of Major-General L. J. Blenkinsop, C.B., D.S.O., Director-General of the Army Veterinary Service, several observations were made for me; likewise Principal Bradley, M.D., D.Sc., and the members of the staff at the Royal (Dick) Veterinary College, Edinburgh; and Captain J. T. Edwards, B.Sc., of the Royal Veterinary College, London. Dr. A. S. Lea, F.R.S., who so willingly took over the duties of critic and proof-reader of the previous editions, has, to my great regret, since died; but I have been happily fortunate in securing the assistance of Mrs. F. Bullock, M.A., who, besides relieving me of the labours of proof-reading and indexing, has given me the advantage of her critical judgment. For her valuable co-operation I tender my most sincere thanks. The student is urged to consult her index, as in a work of this kind it is impossible, excepting through this channel, to bring together the many scattered references bearing on the same subject.



PROFESSOR G. COLIN.

My thanks are also due to those authors and publishers who have been good enough to permit reproductions of illustrations from their works, all of which are acknowledged in the text.

Finally, I recognise that the time has arrived, or is fast approaching, when my work must close and younger men take up the subject. I observe with great regret that there appears a disinclination in the young school to specialise in physiology, in which case it will pass into the hands of others outside the profession, who will be unable to draw the necessary practical lessons, owing to their ignorance of clinical matters. Pure physiology is one thing, but what the practitioner requires is physiology in its application to disease, and it cannot be said that the fringe of this question has yet been touched; it can only be done by those whose training renders them familiar with the habits and diseases of animals. Pathology has been happily defined as 'physiology out of health,' and the chief reason why we study the functions of the normal body is to be enabled to apply the information thus obtained to the study of disease.

F. S.

December, 1920.

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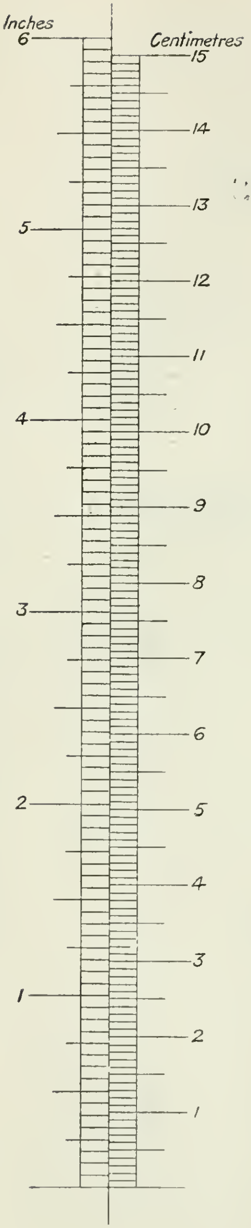
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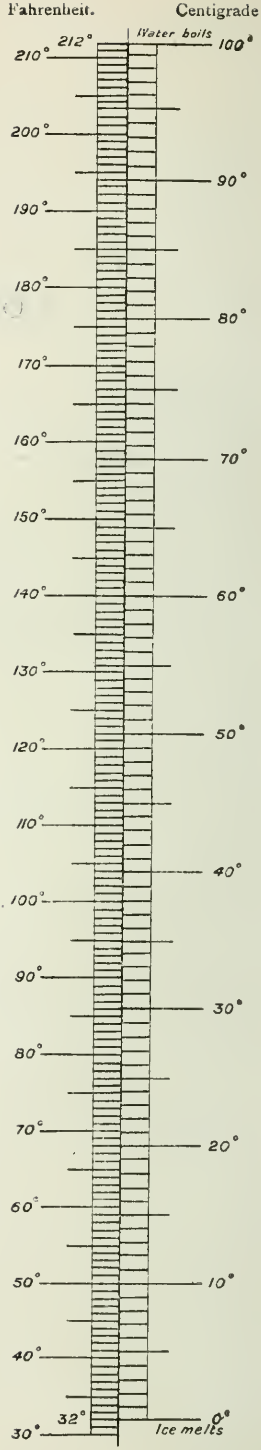
Fahrenheit.
Centigrade
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Water boils
100°
210°
200°
90°
190°
180°
80°
170°
160°
70°
150°
140°
60°
130°
120°
50°
110°
40°
100°
90°
30°
80°
70°
20°
60°
50°
10°
40°
32°
0°
30°
Ice melts

A MANUAL OF VETERINARY PHYSIOLOGY

CHAPTER I

THE BLOOD

THE special functions of the blood are to nourish all the tissues of the body, and thus aid in their growth and repair; to furnish material for the purpose of the body secretions; to supply the organism with oxygen, without which life is impossible; and finally to convey from the tissues the products of their activity. To enable all this to be effected the blood is constantly in circulation, is rapidly renewed, is instantaneously purified in the lungs, and, by means of certain channels, is placed directly in communication with that nourishing fluid absorbed from the intestines by which it is constantly repaired.

Physical Characters.—Blood is a red, opaque, rather viscous fluid, the tint of which depends upon whether it is drawn from an artery or a vein; in the former it is of a bright scarlet colour, whilst in the latter it is of a purplish red. The colour is due to a pigment called hæmoglobin contained in the red corpuscles. Whether the colour is scarlet, as in blood from an artery, or purplish, as from a vein, depends on the amount of oxygen with which the hæmoglobin is combined.

The **reaction** of blood, as tested by glazed litmus paper, is always distinctly alkaline. When, however, the **true reaction** of the fluid is determined by modern methods it is found to be only very slightly alkaline. The principle of the method employed for the accurate determination of the blood reaction is based upon the fact that in all aqueous solutions the product of the hydrogen-ion and the hydroxyl-ion concentrations is a constant—namely, the ionisation constant of water, usually stated in the following form, the enclosures in brackets denoting gramme-ionic concentrations per litre:

$$[H^+] \times [OH^-] = K = 10^{-14} \text{ (approximate).}$$

In neutral solutions the $[H^+]$ and $[OH^-]$ are equal—namely, 1×10^{-7}. In acid solutions the $[H^+]$ is greater and in alkaline solutions less than the $[OH^-]$. If, therefore, either the hydrogen-ion or the hydroxyl-ion concentration can be determined, the *true reaction* of the fluid stated in terms of $[H^+]$ or $[OH^-]$ can be accurately expressed.

The modern method consists in the determination of the hydrogen-ion concentration of the blood, making use of the hydrogen electrode, and the concentration values so arrived at are usually stated in terms of the negative exponent with the symbol P_H, the minus sign being omitted. P_H 7·5 is therefore another form of $1 \times 10^{-7·5}$, and would denote a slightly alkaline fluid such as blood, while P_H 6 would signify a slightly acid fluid such as urine. A rise in the P_H value signifies an increase in alkalinity. In order to gain an idea of the actual concentration of the hydrogen-ions in blood, it is advisable to state it directly rather than in logarithmic form; thus P_H 7·35, which may be regarded as an average value for blood, equals $0·446 \times 10^{-7}$, or 0·0000000446 gramme hydrogen per litre of blood. The reaction of blood is mainly dependent upon the ratio of carbonic acid to bicarbonate, $\frac{H_2CO_3}{NaHCO_3}$. One of the most important properties of blood is the maintenance of a fairly constant reaction, although the exchange between the tissues and the blood must result in the entrance and removal of acid and basic radicles. The mechanisms which contribute to the regulation of the reaction are extremely important. These are in part intrinsic to the blood itself, the so-called 'buffer salts,' of which by far the most important is sodium bicarbonate. These buffer salts may be regarded as soaking up the added H^+ or OH^--ions.* In addition, the respiratory mechanism and the kidneys regulate the reaction, the former responding to a rise in the hydrogen-ion concentration by an increased pulmonary ventilation, and so removal of the carbonic acid, the latter by an excretion of a more acid urine. Recently much valuable work has been done on the bicarbonate or alkali reserve store of the blood, and the effect of various conditions upon it, such as shock, hæmorrhage, diabetic coma, etc.

Excepting in the herbivora, considerable amounts of acid may be administered by the mouth or formed in the tissues without affecting the reaction of the blood, the acid being neutralised by the ammonia split off from proteins. Proteins may, in fact, act in a dual capacity, either as bases neutralising acidity, or as acids neutralising alkalinity.

---

* The expression 'buffer salts' is intended to indicate the fact that they prevent the shock to the reaction of the blood on the addition of acid or alkali. Bayliss thinks the term ought to be avoided, and points out that it originally arose through a mistranslation of the word 'tampon' employed by the French writer who first dealt with the question. He used it to indicate that the sodium bicarbonate soaked up the excess of acid or alkali.

The carbon dioxide of the blood is in the main united with bases, especially soda, and the total carbonic acid content of a sample of blood is a measure of its capacity not only for carrying carbonic acid, but also for maintaining the normal reaction of the blood. In the herbivora the carbonic acid content is readily reduced under the influence of acids administered by the mouth or formed in the body, and the protective mechanism is thus reduced.

The recently-drawn blood of the cat and dog has a peculiar and decidedly disagreeable **smell**; this is not observed in the blood of the horse and ox. The **taste** of blood is saltish, due to the amount of sodium chloride it contains.

The **specific gravity** varies in different animals: in the horse, ox, and pig, 1·060; in the sheep, 1·050 to 1·058; in the dog, 1·050 (Colin). According to Hoppe-Seyler, the specific gravity of the liquor sanguinis of the horse is 1·027 to 1·028, and the specific gravity of the cells 1·105. This considerable difference between the specific gravity of the cells and the liquor sanguinis in the horse accounts for the rapid manner in which the cells sink in horse's blood when drawn from the body, producing during the process of clotting the so-called 'buffy coat.'

The **viscosity** of the blood is an important determining factor regulating the blood-pressure and velocity. Thus the substitution of simple saline solutions for whole blood, such as would occur in intravenous injection after hæmorrhage, results only in a very temporary rise in blood-pressure, while the addition of a colloid—for example, gum arabic—to the saline not only raises the pressure immediately after injection, but enables the pressure to be maintained at the higher level. The osmotic pressure of the colloid is also of great value, as, owing to the fact that the capillary walls are practically impermeable to colloid, the filtration or loss of water from the vessels is checked by the counter-osmotic effect.

The viscosity of blood is four or five times greater than that of water. It is rather higher in the dog and cat than in man.

Composition of the Blood.—Blood consists of a fluid portion or plasma and of the blood cells or corpuscles suspended therein.

Plasma, or **liquor sanguinis,** is a yellow-coloured, somewhat viscid, fluid, containing in solution—

Protein.
Extractives.
Mineral matter.
Enzymes.
Unknown substances (*i.e.*, immune bodies).
(See p. 10.)

The **corpuscles** are—

Red corpuscles, or erythrocytes.
White corpuscles, or leucocytes.
Platelets.

So far as the presence of the various constituents is concerned, the blood of any one animal presents a very uniform character, but their proportions in the blood of different animals are liable to great variation. The composition of the blood is also affected according to the source from which it is derived; the blood from an artery is not exactly like that from a vein.

Plasma forms about 66 per cent. of the blood; and consists of three proteins, which are held in solution—viz., *fibrinogen, paraglobulin* (*serum-globulin*), and *serum-albumin*. The two former belong to the globulin group of proteins; the latter to the albuminous group, of which egg-albumin is typical.

The three proteins may be separated by the employment of certain neutral salts. **Serum-albumin** is precipitated by saturation with ammonium sulphate. Its solution in a neutral or acid medium is thrown down by heat. The temperatures of coagulation, 70° to 75° C. (158° to 167° F.), would appear to indicate that there are two or three different proteins classed together as serum-albumin.

This substance is found not only in blood-plasma, but in lymph. It also forms a part of such secretions as milk. Its source is believed to be the protein substances of the food which are taken up from the intestinal canal, though there is no experimental proof of the correctness of this view. Serum-albumin obtained from the blood of the horse may readily be made to crystallise.

Paraglobulin, or serum-globulin, is distinguished by being precipitated by saturation with magnesium sulphate, or half saturation with ammonium sulphate. In neutral or faintly acid solutions it is coagulated by heating to 75° C. (167° F.), and there is reason to think from the behaviour under analysis of the paraglobulin obtained from serum that this substance is probably a mixture of two or three allied proteins. It is supposed that the source of paraglobulin is twofold—first the protein substances of the food, and secondly the disintegration of the white cells of the blood; but in both cases proof is wanting.

Bayliss draws attention to the fact that the serum proteins of the blood are remarkable for being chemically very inert substances. They do not serve for the nutrition of the tissues, but their chief function, apart from the important share they take in the process of clotting, appears to be to give a viscosity to the blood, so that this shall not lose water to the tissues too rapidly.*

Fibrinogen constitutes but a small proportion of the total protein of plasma. It is precipitated from solution by half saturation with sodium chloride. It belongs to the group of proteins known as globulins, and is a substance of remarkable interest, for on its conversion from a fluid to a solid condition depends the phenomenon of the coagulation of the blood. Like the other proteins in plasma, it coagulates on heating, but at a much lower temperature, for fibrinogen is coagulated at 56° to 60° C. (133° to 140° F.). Blood so treated is no longer capable of clotting, owing to its fibrinogen being coagulated. The source of fibrinogen in the body is unknown; it is supposed to be connected with the destruction of leucocytes, and there is also some evidence of the liver being concerned in its formation.

Perhaps the nearest approach to pure plasma is the fluid found in the pericardial and abdominal cavities. That which is effused into the chest during an attack of pleurisy is plasma to start with, but if it has undergone coagulation and fibrin (false membranes) has been formed, then the resulting fluid is serum.

In the following table is shown the composition of the blood plasma of different animals. The figures are expressed as grammes in 100 c.c. of blood. It will be observed that in the horse the globulins exceed the albumins, while in the dog and pig the reverse holds good. The poverty of dog's blood in total proteins, as compared with that of the horse and pig, is also striking.

	Total Proteins.	Serum-Albumin.	Para-globulin.	Fibrinogen.
Dog - - - -	6·03	3·17	2·26	0·60
Sheep - - - -	7·29	3·83	3·00	0·46
Horse - - - -	8·04	2·80	4·79	0·45
Pig - - - -	8·05	4·42	2·98	0·65

So long as the blood is in circulation or prevented from clotting, its fluid portion is termed 'plasma'; but if blood be allowed to coagulate, in course of time it separates into a solid clot and a liquid portion, and this liquid is no longer known as plasma, but as serum. **Serum** is therefore plasma which is modified as the result of coagulation, and as this latter process is attended by the production of fibrin, it may be said that serum is plasma minus the fibrin-forming elements.

Serum does not contain fibrinogen, for the reason that the latter has been used up in the process of clotting, but it possesses, in addition to serum-albumin and paraglobulin, a body known as *fibrino-globulin*, believed to be split off from fibrinogen in the act of clotting, and *nucleo-protein*, supposed to be derived from the fibrin ferment; some observers doubt the existence of this latter substance in the serum. The total protein content of serum is 8 or 9 per cent., and thus resembles the protein content of plasma; the extractives and salts are the same in both fluids.

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* *British Medical Journal*, June 29, 1918.

In the following table a comparison is made between the proteins of plasma and serum:

Plasma.	Serum.
Serum-albumin.	Serum-albumin.
Paraglobulin.	Paraglobulin.
Fibrinogen.	Fibrino-globulin.
	Nucleo-protein.

Corpuscles.—Blood examined under the microscope is found to contain an enormous number of bodies termed 'corpuscles' floating in the liquor sanguinis. These corpuscles are of two kinds, red and white; the former are the more numerous, the latter are the larger.

The **Red Corpuscles** constitute 33 per cent., or one-third of the total blood. Viewed under the microscope, they are found to be biconcave discs, circular in shape, and possessing no nucleus (Plate I.); they are soft, flexible, elastic bodies, capable of having their shape readily altered by pressure, and this enables them to pass along the finest capillaries. The colour of a single corpuscle is yellow, but when heaped together they appear red, and thus give the colour to the blood.

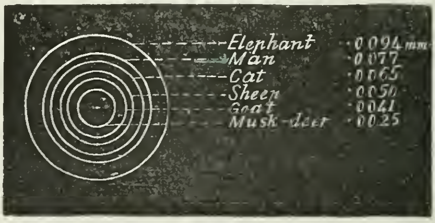

FIG. 1.—DIAGRAM SHOWING RELATIVE SIZE OF RED CORPUSCLES OF VARIOUS ANIMALS (STEWART).

In all mammals, excepting the camel tribe, the red cells are circular and biconcave; in the Camelidæ they are elliptical and biconvex. In all vertebrates below mammals they are biconvex, oval, and nucleated (Plate I.). The corpuscles vary in size in different animals, being smallest in the deer tribe and largest in the elephant, the relative sizes being shown in Fig. 1.

When a drop of blood is shed, the red cells at first move quite freely each over the other. In a short time they tend apparently to become sticky, and when this state is reached they have a tendency to lie in long rows, with their flat surfaces in close contact, their appearance resembling that of a pile of pennies. This condition is not marked in horse's blood.

A red blood-cell is composed of a spongy stroma, holding in its meshes the red colouring matter. The stroma or framework of the corpuscle consists of nucleo-albumin, lecithin, cholesterin, and salts; the red colouring matter, hæmoglobin, forms no less than 32 per cent. of the total solid matter of the living corpuscle.

Great discussion has taken place as to whether the corpuscle is a perforated mass of protoplasm containing no covering, or whether it possesses a cell-wall, as its microscopical appearance indicates. At present the general feeling is that there is no cell-wall, but that there is a condensation of the cell-substance at the periphery, while within the spongy substance of the interior is lodged the hæmoglobin, probably in an amorphous condition, certainly not in a crystalline state, and perhaps not in solution. It is further supposed that the large amount of lecithin and cholesterin present in the stroma determines the nature and degree of the permeability of the external layer of the cell. For example, water, alcohol, ether, and a solution of urea can pass in, but not neutral salts.

The number of corpuscles in the blood is determined approximately by the method either of Gowers or Malassez. The principle on which these methods are based is the same—a known quantity of blood is diluted with a known bulk of artificial serum and thoroughly mixed; of this a small drop is placed in a counting-chamber of known capacity, which is ruled into squares, and examined under the microscope. The blood-cells occupying the squares are counted, as may readily be done, and the mean of them taken. In the horse the mean number of red blood-corpuscles per cubic millimetre is 7,212,500, and in the ox 5,073,000. Taking the amount of blood in the horse as 29 litres (50 pints, or 66 pounds), this gives 204,113,750,000,000 as the approximate number of red cells in the body (Ellenberger).* It is evident that a loss of water from the blood means a larger relative proportion of red cells present, while an excess of water, by diluting the blood, would show a loss of red cells; thus the number of the red cells is increased by sweating, by the excretion of water from the bowels and kidneys, and by starvation, while it is diminished by copious draughts of water, also by pregnancy. But apart from these conditions, it is undoubted that an actual increase or decrease in the number of red cells may occur, this

* 'Physiologie der Haussäugethiere.'

numerical variation being especially marked in some diseases. The shape of the red cell is affected by the amount of fluid in the plasma; if the latter be artificially concentrated, water diffuses from the corpuscle to the plasma, and in consequence the corpuscle itself shrinks and becomes wrinkled (Plate I.). If the plasma be diluted, the red cells swell. A 0·9 per cent. solution of sodium chloride causes the corpuscles neither to shrink nor swell; this strength is known as ' physiological salt solution ' (an isotonic solution), and may be employed for the purpose of transfusion.

Each red cell offers a certain absorbing surface for oxygen, which, if calculated on the total number of corpuscles, is something enormous, being equal for the horse to a square having a side of 164 metres (180 yards). The opacity of blood is due to the red cells reflecting light as the result of their peculiar shape; if the cells be destroyed, the blood becomes transparent or, as it is termed, ' laky,' of which more will presently be said.

The greater part of the red cell consists, as already stated, of hæmoglobin, a substance possessing a remarkable affinity for oxygen; this it obtains at the lungs, and leaves behind in the tissues. The hæmoglobin of the red cells, therefore, exists in two states, one in which it is charged with oxygen called ' oxyhæmoglobin,' and the other in which it has lost its oxygen and is known as ' reduced hæmoglobin,' or simply hæmoglobin. The process of oxidation in the lungs and reduction in the tissues is constantly occurring at every cycle of the circulation, with the ultimate result that the red blood-disc, the life of which is probably only a matter of a few days, gets worn out and dies. In this condition it is cast off from the system, being got rid of through the medium of the liver. In addition to the blood-stream, other seats of destruction are suggested—viz., the spleen, bone-marrow, and lymph-glands—but no definite statement can at present be made. When the red cells die, their hæmoglobin is set free, and decomposed into an iron-free residue from which, probably, all the pigments of the body are formed, certainly those of the bile.

The seat of formation of the red cells is in the red marrow of bones, where they are formed from certain nucleated colourless cells; there are several varieties of blood-forming cells (*erythroblasts*) in the red marrow, and it is not definitely settled which of these furnish the red blood-cells. All other seats of formation are doubtful. In the embryo the future red cells for a certain period are nucleated and contain no hæmoglobin, but these are gradually replaced by non-nucleated, hæmoglobin-holding corpuscles before birth. It is interesting to observe that both in the embryo and in the adult the red cells are derived from a nucleated precursor.

By the time the corpuscle takes its place in the blood as a cell which has lost its nucleus it is on the downward path. This and other considerations have caused its probable life in the blood-stream to be estimated at only a few days.

Hæmolysis.—It has been pointed out that in a normal condition the hæmoglobin is contained wholly within the red cells, and that there is no passage of colouring matter from the cells to the fluid in which they are carried. Anything which kills the red cell, or, if we adopt the cell-wall view, anything which breaks down the envelope, allows the hæmoglobin to escape.

The cells may be destroyed by alternately freezing and thawing the blood, or by the passage through it of electric shocks, or by the addition of certain agents such as chloroform, ether, bile salts, tannic or boric acids, etc. The hæmoglobin becomes liberated from the broken-up cells, and stains the naturally yellow plasma a red colour. The blood under these circumstances, as we have seen, is no longer opaque, but transparent, and the term 'laky' well describes its appearance. The entire process is described as 'hæmolysis.'

Most of the above causes of hæmolysis act as protoplasmic poisons; they kill the cell, and as the osmotic pressure of the plasma is slightly less than that of the corpuscular contents, the hæmoglobin diffuses out. Poisons such as ether and chloroform are probably hæmolytic owing to their chemical effect in dissolving the cholesterin and lecithin of the corpuscles. Other poisons may unite with these substances and render them soluble, by which means hæmoglobin escapes from the cell. Snake venom and the poison of bees and of certain spiders produce hæmolysis, so also some pathological toxins, of which the most noteworthy in the horse is that producing so-called *azoturia*. The most remarkable example of hæmolysis is that produced by adding to, or injecting into, the blood of one animal the serum of an animal of a different species. This leads in certain cases to destruction of the red cells, and a chain of results of the highest practical importance. If, for example, the fresh serum of the blood of the dog be added to the washed red corpuscles of the rabbit, the latter are destroyed and the colouring matter liberated. If the serum of the dog be previously heated to 55° C. (132° F.), it may be added in any quantity to the washed blood-cells of the rabbit, without producing any effect on them; evidently something has been destroyed by the process of raising the temperature. This something can be restored by adding to the heated dog's serum some serum which is not hæmolytic for rabbit's cells (say rabbit serum). The effect now is to render the dog's serum once more hæmolytic.

So far the phenomenon is physiological. The serum of any animal, however, can be rendered hæmolytic for the corpuscles of another species by injecting the first with the red corpuscles of the second. If, for example, the corpuscles of species A, say an ox, be injected into species B, say a goat, the serum of the goat becomes actively hæmolytic for the corpuscles of the ox, and will cause hæmoglobinuria and death when inoculated to the latter animal. The goat's serum will also hæmolyse the corpuscles of the ox *in vitro*. If it be heated to 55° C., however, it loses its hæmolytic action, which can be restored to it in the way mentioned above. The explanation is that there are two substances in the hæmolytic serum concerned in the production of hæmolysis. One is relatively unstable, and is destroyed by a temperature of 55° C. This is the destroying agent, which is known as the *complement*. The other substance is spoken of as the *immune body*, the *antibody*, the *amboceptor*, or *substance sensibilisatrice*. It is not destroyed by a temperature below 65° C. When a hæmolytic serum is heated to 55° C. for half an hour, its hæmolytic action is lost, because the complement has been destroyed. It can be restored by adding fresh, though non-hæmolytic, serum from another animal—a guinea-pig, for example—because the complement is not specific, and is the same in all animals. If a hæmolytic serum be heated before injection into the animal, it still causes hæmolysis, because the complement is supplied by the animal's serum. The immune body, on the other hand, is specific for the corpuscles of the species against which it has been prepared, and for those of no other. These phenomena are closely related to the reaction of the body towards bacteria, and are concerned in the production of antitoxins.

Agglutination is the process by which the red blood-corpuscles are collected together in clumps, under the influence of an agent in the blood known as an *agglutinin*. Agglutination frequently precedes hæmolysis, but it is independent of it, for if the *complement* of a hæmolytic serum be destroyed by heating to 55° C., the agglutinating substance remains, being relatively unaffected by heat.

If an animal, say a rabbit, be injected with the blood-cells of the dog, the serum of the rabbit, which normally has no effect on the blood-cells of this animal, becomes powerfully hæmolytic for dog's corpuscles, and, further, it agglutinates for the corpuscles of the dog. An agglutinin has, therefore, been experimentally produced in the serum of the rabbit. The phenomenon of agglutination is employed in bacteriology as an important aid to diagnosis.

Precipitins.—If the serum of one animal be injected into an animal of a different species, it is found that the serum of the receiver is capable of causing a precipitate in the normal serum of the donor; for example, if a rabbit be injected with the serum of a dog, the rabbit serum will in course of time produce a precipitate if added to dog's serum, but not if added to the serum of any other animal. Such substances are known as *precipitins*, and are employed for the purpose of identifying different bloods and for other purposes. They may, for example, be used for the determination of the flesh of different animals—horse-flesh, for instance, when sold as beef; for if a rabbit be injected with an extract of horse-flesh, its serum will produce a precipitate with extracts of horse-flesh, but not of ox-flesh.

Blood Platelets.—These may be seen in the circulating blood, but more easily in blood which has been shed—certain small colourless cells one-quarter the size of a red corpuscle, and usually of a round or oval shape. In shed blood they agglutinate and rapidly disintegrate, but under suitable conditions they may be kept alive, when they exhibit amœboid movements. At one time they were regarded as disintegration products of the red cells, but this view is no longer held, and it is probable they are distinct cellular elements. Of their function little or nothing is known, but that they play an important part in blood-clotting is undoubted.

Hæmoglobin is the red colouring matter of the blood, and is remarkable for being one of the most complex substances in organic chemistry. It contains the elements C, H, O, N, S, and Fe. The molecule of hæmoglobin is probably the largest of any known substance which is capable of being crystallised. If, as is most usually assumed, its molecule contains one atom of iron, then, on this assumption, and from a knowledge of its percentage composition, the molecular formula for the hæmoglobin of dog's blood may be represented as $C_{758}H_{1203}N_{195}S_2FeO_{218}$, which is some 16,000 times that of a molecule of hydrogen. It has been supposed that the size of the hæmoglobin molecule is connected with the heavy atom of iron which it has to carry. The function of the iron is closely connected with the power the pigment has of combining with oxygen. This compound of oxygen-hæmoglobin constitutes a chemical system peculiar to itself, for there is no other like it known.

Hæmoglobin is a protein, but is distinguished from the majority of the other members of its class by the comparative ease with which it may be obtained in a crystalline form; while, on the other hand, its behaviour in a dialyser is not that of a crystalloid, but that of a colloid.

Hæmoglobin, under the influence of heat, acids, or alkalies, is broken up in the presence of oxygen into a simple protein, *globin*, and a pigment, *hæmatin*. It is therefore a compound of a protein body with hæmatin; the protein portion of the molecule represents the greater part, the pigment being only 4 per cent. of the total. In the protein portion is found all the sulphur, and in the pigment all the iron of the molecule. The pigment hæmatin exists in the living blood as hæmoglobin, the great difference between these two substances being that hæmatin forms a stable, while hæmoglobin forms a feeble combination with oxygen.

The union of oxygen with hæmoglobin gives a true chemical compound, 1 gramme ($15\frac{1}{2}$ grains) of hæmoglobin uniting with 1·34 c.c. (0·08 cub. in.)of the gas, and forming **oxyhæmoglobin.** This is not a stable compound; it readily gives off its oxygen either in the presence of oxidisable substances, or in an atmosphere free from oxygen, and by so doing becomes **reduced hæmoglobin.** Other conditions which cause hæmoglobin to readily part with its oxygen are a relatively high temperature, such as that of the blood, and the presence of salts and acids, especially carbon dioxide. It is oxyhæmoglobin which gives the bright colour to arterial blood, and it is the presence of partly reduced hæmoglobin which gives the darker tint to venous blood. The change in colour which venous blood undergoes on exposure to the air is due to the absorption of oxygen by hæmoglobin. By a similar absorption the blood is charged with oxygen in the lungs, brought back to the heart, and distributed all over the body to the tissues, where it gives up the bulk of its oxygen, and as partially reduced hæmoglobin is brought back by the veins to the heart for distribution to the lungs, where it renews its oxidised condition. Excepting in the latest stages of asphyxia, hæmoglobin is never completely reduced in the body.

Oxygen is not the only gas with which hæmoglobin is capable of forming a chemical compound. Carbon monoxide unites with it more readily than oxygen, forming the definite compound **carbonic oxide hæmoglobin.** In great contrast to oxyhæmoglobin, this is a remarkably stable compound, the carbon monoxide holding so tenaciously to hæmoglobin that oxygen cannot displace it. This explains the highly poisonous nature of this gas. The spectrum of CO hæmoglobin closely resembles that of oxyhæmoglobin (see Fig. 2). A still more poisonous compound is **nitric oxide hæmoglobin,** since this gas is attached to the hæmoglobin even more tenaciously than carbon monoxide.

Hæmoglobin also forms an important compound with carbon dioxide. This compound may be formed even when the hæmoglobin is already nearly saturated with oxygen; the explanation which has been offered is that, while the oxygen is united to the pigment portion of the molecule, the carbon dioxide is united to the protein portion. Buckmaster has shown that hæmoglobin can unite with large quantities of carbon dioxide and give it off again at a lower pressure.

When examined spectroscopically, oxy- and reduced hæmoglobin produce quite distinctive spectra, by which they may be readily recognised. To state the matter broadly, oxyhæmoglobin gives two well-marked dark absorption bands or shadows in the green portion of the spectrum, one band being wide, the other narrow, while reduced hæmoglobin gives one wide single band in nearly the same position (Fig. 2). The change from oxyhæmoglobin to reduced hæmoglobin may readily be brought about in spectroscopic examination by the addition of an alkaline solution of ferrous tartrate (Stokes's fluid) to the blood.

Crystals of hæmoglobin, when seen in bulk, are of a dark red or bluish-red colour; they are extremely soluble in water, the solution being dichroic—viz., green by reflected and bluish-red by transmitted light. The blood of the horse, cat, dog, and guinea-pig readily yields crystals of oxyhæmoglobin; that of the ox, sheep, and pig crystallises with difficulty. The crystals are generally rhombic prisms or needles, but the form differs according to the animal (Fig. 3). Reduced hæmoglobin can be crystallised only with great difficulty, and in an atmosphere free from oxygen.

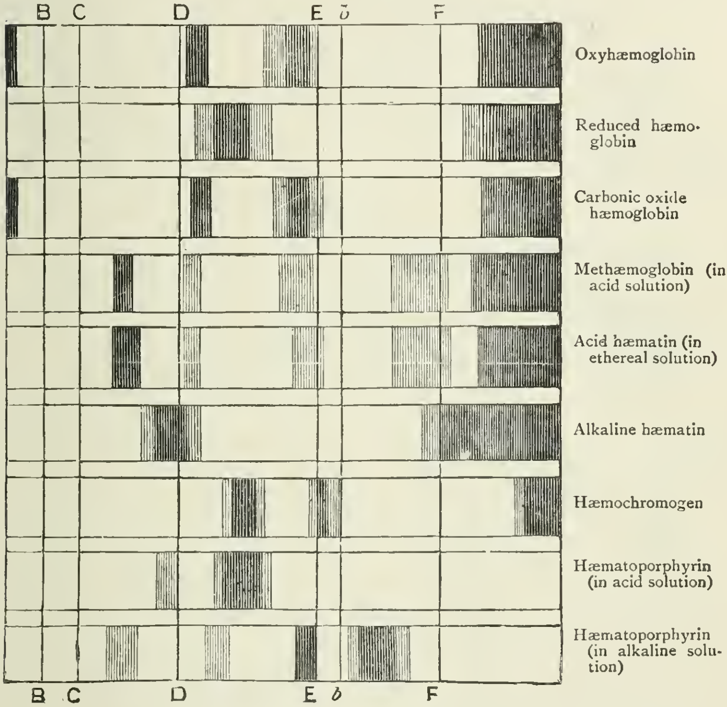
B
C
D
E
b
F
Oxyhæmoglobin
Reduced hæmoglobin
Carbonic oxide hæmoglobin
Methæmoglobin (in acid solution)
Acid hæmatin (in ethereal solution)
Alkaline hæmatin
Hæmochromogen
Hæmatoporphyrin (in acid solution)
Hæmatoporphyrin (in alkaline solution)
B
C
D
E
b
F

Fig. 2.—Table of Spectra of Hæmoglobin and its Derivatives (Stewart).

The total amount of hæmoglobin in a horse's body is about 4 kilogrammes (8·8 pounds), and the amount of iron contained in this is about 17 grammes (257 grains). This calculation is based on the assumption that the amount of blood in the body is 29 litres (50 pints).

In dried red blood-cells hæmoglobin exists in the proportion of 90 to 94 per cent., in the corpuscle under normal conditions it represents 32 per cent. of its weight; in the total blood of the horse it forms 13·15 per cent., in the ox 9·96 per cent., in the sheep 10·34 per cent., in the pig 12·7 per cent., and in the dog 9·77 per cent. (Ellenberger).* The younger the animal the less hæmoglobin; males have more than females, and castrated animals more than entires (G. Müller).†

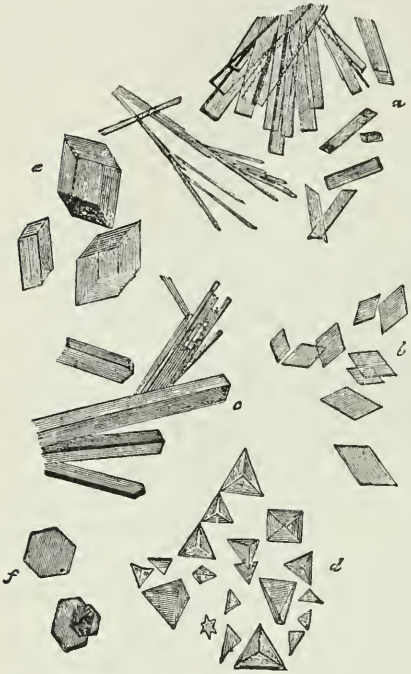

Fig. 3.—Oxyhæmoglobin Crystals.

a, *b*, From man; *c*, from cat; *d*, from guinea-pig; *e*, from hamster; *f*, from squirrel (Frey).

The functions of hæmoglobin cannot be studied until the subject of respiration is dealt with.

Methæmoglobin is a derivative of hæmoglobin, and may be produced by allowing blood to be exposed to the air until it becomes brown in colour; or it may be prepared by the action of ferricyanide of potassium or nitrite of amyl, etc., on oxyhæmoglobin. This substance contains the same amount of oxygen as hæmoglobin, but it will not part with it, excepting in the presence of reducing agents; for respiratory purposes it is therefore useless. It is not a normal constituent of the blood, but may be found in the urine whenever a sudden breaking-down of red corpuscles occurs, as, for example, in the so-called azoturia of the horse. Its spectrum is seen in Fig. 2.

Hæmatin, as one of the decomposition products of hæmoglobin, has been previously referred to. It will be remembered that it is obtained by decomposing hæmoglobin by boiling, or the addition of alkalies, acids, or acid salts; in either case the hæmoglobin splits up into a substance containing the iron, known as

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* 'Physiologie der Haussäugethiere.'

† *Ibid.*

hæmatin, and a protein substance or substances termed **globin.** Hæmatin in the dry state strongly resembles iodine in appearance; it has a metallic lustre, a blue-black colour, is not crystallisable, and yields, when pulverised, a dark brown powder which contains 8·82 per cent. of iron. It is a remarkably stable substance and the colouring matter presents a distinctive spectrum both in an acid and in an alkaline solution (see Fig. 2). Alkaline solutions of hæmatin can take up and give off oxygen as does hæmoglobin. When hæmatin is treated with glacial acetic acid and common salt, it yields **hæmin** or hæmatin hydrochloride, which, when examined microscopically, is found to consist of prismatic crystals, dark or nearly black in colour (see Fig. 4). Hæmin crystals may be readily produced by warming the dried blood with a drop of glacial acetic acid on a slide; this fact is used as a microscopical test.

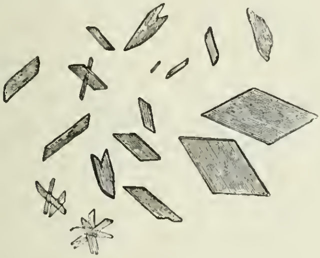

FIG. 4.—CRYSTALS OF HÆMIN (FREY).

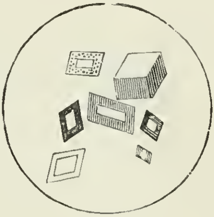

FIG. 5.—CRYSTALS OF HÆMATOIDIN (STEWART).

When reduced hæmoglobin is decomposed by acids or alkalies, oxygen being carefully excluded, it yields **hæmochromogen,** a substance presenting a definite spectrum; this test is employed in the detection of old blood-stains (see Fig. 2). **Hæmatoporphyrin** is obtained by the action of strong sulphuric acid on hæmatin, which thereby loses its iron; hæmatoporphyrin is really hæmatin from which the iron has been removed; it is isomeric with bilirubin. The spectrum of this substance in acid and alkaline solutions may be seen in Fig. 2.

Hydrobilirubin is obtained by the action of reducing agents on hæmatin; it very closely resembles urobilin, a pigment found in urine.

Hæmatoidin (Fig. 5) is found in old blood-clots and in the ovary; it is a crystalline iron-free product derived from hæmatin, and gives the same reaction with nitrous acid as bile pigment—viz., a play of colours. Hæmatoidin is, in fact, chemically identical with bilirubin, and the name is now of interest merely as indicating the close genetic relationship of the pigments of bile to the colouring matter of blood. Notwithstanding this close relationship, it has not as yet been found possible to convert hæmatin into bilirubin. The nearest approach to bilirubin is iron-free hæmatin (hæmatoporphyrin). Again, both hæmatin and bilirubin may be made to yield an identical product (hydrobilirubin); this product closely resembles urobilin, a pigment found in the urine, and urobilin beyond all doubt is derived from bilirubin in the digestive canal, under the influence of putrefactive organisms.

White Corpuscles, or Leucocytes.—There are certain corpuscles found in the blood, lymph, connective tissue, and in pathological products such as pus, which possess a great family resemblance. In the blood they are known as 'white corpuscles,' and it seems quite certain that between the blood and the tissues a free interchange of corpuscular elements occurs; this process is exaggerated under pathological conditions, as in the case of inflammation and suppuration.

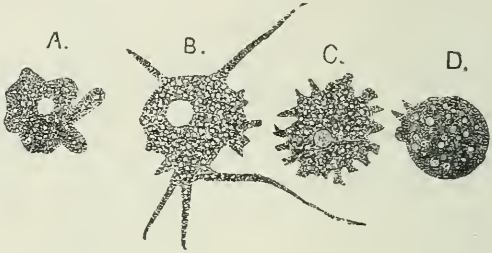

FIG. 6.—AMŒBOID MOVEMENT (STEWART).

A, B, C, D, Successive changes in the form of an amœba.

One characteristic of these cells is their power of spontaneous movement—'amœboid,' as it is termed. In Fig. 6 successive changes in the form of an amœba are shown, and very similar changes occur in these cells. These changes in shape assist materially in the passage of the corpuscle through the walls of the vessels into the tissues. In consequence of their migratory habits these cells are frequently referred to as wandering cells. The white cells of the blood are so called in contradistinction to the coloured or red cells, compared with which they exist in the proportion of 1 to 300-700, depending on the source of the blood. The white cells at the present time are more frequently referred to as blood-leucocytes. They are not all of one kind; there are microscopical differences in their structure which has enabled a classification to be made, and though this is by no means final, particularly in view of the limited knowledge possessed regarding these cells, yet it is useful as a means of identification and description. Ehrlich regards the white corpuscles as divisible into two main groups—*lymphocytes* and *leucocytes*. The former are distinguished by the cell-body being free from granules, while amœboid movement may be absent. The opposite condition exists in leucocytes.

Two varieties of **Lymphocytes** are found in the blood—*small* and *large*. The former, the size of a red cell, is represented by about one-quarter of all the white corpuscles; the latter, two or three times larger in size, do not represent more than 1 per cent. of the whole number of white corpuscles.

Three varieties of **Leucocytes** are described—*polynuclear*, or *polymorphonuclear*, which represent the bulk of the white blood-cells, with a sub-group known as *eosinophiles* ; *uninuclear* occurring to the extent of from 2 to 10 per cent. of the white cells; and *mast-cells*, which represent less than 1 per cent. Not only the nature of the nucleus, but also the reaction which the cell granules give with dyes, enables these groups to be distinguished from one another. The granules of the uninuclear cell readily stain with neutral dyes; the polynuclear cells stain with neutral or acid dyes, while the mast-cells demand basic dyes. Some leucocytes and lymphocytes may be seen in Plate I., 2.

The origin of the lymphocytes and leucocytes has been variously attributed to lymphatic tissue and bone-marrow, but very little is at present known of the subject. There is a free communication between the lymphatic system and the blood via the thoracic duct, and though a mixture of material gains access to the blood by this route, there is no doubt that much of it is pure lymph.

The white corpuscles contain about 10 per cent. of solids. The cell protoplasm consists of proteins belonging to the globulin and nucleo-protein groups, while the nucleus consists of nuclein, which is remarkable as being a very stable substance, and also as containing phosphorus. The effect of nucleo-protein when injected into the circulation will be dealt with at p. 23.

The white corpuscles, as well as the red, are constantly being used up and as constantly replaced. They also possess, as we have seen, the power of passing through the walls of the vessels into the surrounding tissues, from which they are removed by the lymph-channels, and so find their way back to the blood. No doubt many corpuscles leave the blood, for whose destruction we are unable to account, but it is suggested that by their death they influence the composition of the blood-plasma, as in this fluid their component parts must become dissolved after their death.

During the life of the white corpuscle great activity prevails; it is constantly giving up and taking in material which must affect the composition of the plasma. It is known that the white cell possesses the power of digesting certain substances, both solid and liquid. The researches of Metschnikoff have paved the way towards a better understanding of the probable manner in which protection against certain diseases is obtained. He has shown that the white cells take up the bacteria into their interior and digest them, a process termed *phagocytosis*; it is really a fight between bacteria and leucocytes. The difference in the resisting power to disease possessed by 'fit' over 'unfit' animals, and the greater protection afforded by maturity as compared with youth, are facts which may be directly connected with the question of phagocytosis.

The polynuclear cell above described appears to be the leucocyte best adapted to ingesting bacteria, but all are capable of doing good work, and the thoroughness with which it is done depends upon the composition of the plasma. It appears essential that this should contain a substance which acts upon the bacteria, and renders them an easy prey to the leucocyte. This substance, known as an *opsonin*, may be conveyed to the plasma by the leucocytes, and it may also be artificially increased by the injection into the body of suitable bacteria or of products obtained from them.

It is also probable, as distinct from the doctrine of phagocytosis, that the white cells of the blood may be closely concerned in the production of certain protective substances which destroy bacteria, *bacteriolysins*, the existence of which helps to explain the theory of immunity.

Coagulation.—We are now brought to a consideration of the subject of blood-clotting, a process by which the naturally fluid blood becomes converted into a solid.

If blood be drawn from the body and left at rest, it will be found within a few minutes to have undergone the process of clotting. The fluid first becomes a jelly and then a firm clot or crassamentum, taking a complete cast of the vessel in which it is placed, and so firm in consistence that it may be inverted without any blood being lost. In a short time the clot begins to contract, and by so doing squeezes out a fluid known as *serum* (Fig. 7). This gradually accumulates, and as it becomes abundant the clot sinks. The blood of the horse is remarkable for the slow rate at which coagulation occurs, and the red cells, being specifically heavier than the plasma, have time to fall in the fluid before the process is completed. The result of this is that the upper solid layer is considerably decolourised, forming the so-called **buffy coat**, which, though natural to the blood of the horse, is indicative in other animals of the presence of an inflammatory process in the system.

We have here closely followed the account given by human physiologists of the coagulation of the blood in the horse, but the appearance described is by no means invariable. Coagulation in this animal is often complete in less than five minutes, when, of course, no buffy coat forms, and we are inclined to believe that rapid coagulation and non-buffy coat are the rule rather than the exception; we have repeatedly observed in the case of the horse the formation of the clot to be so rapid as to seem almost instantaneous. One fact in connection with horse's blood is undoubted, and that is that coagulation is more easily slowed or prevented by cold and by neutral salts than it is in the blood of any other warm-blooded animal. May it not be that some confusion has thus arisen, and we have come to regard this abnormally easy slowing of clotting by cold and salts as if it were markedly a characteristic of horse's blood, as it clots naturally?

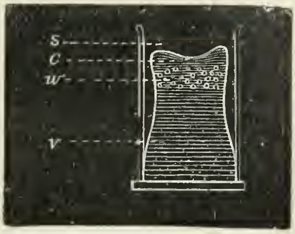

Fig. 7.—Diagram of Clot with Buffy Coat (Stewart).

v, Lower portion of clot with red corpuscles; *w*, white corpuscles in upper layer of clot; *c*, cupped upper surface of clot; *s*, serum.

According to Nasse, the average time occupied in coagulation is as follows:

Pig	½ to 1½ minutes.
Sheep	½ ,, 1½ ,,
Dog	1 ,, 3 ,,
Ox	5 ,, 13 ,,
Horse	5 ,, 13 ,,

In our experience the extreme time mentioned for the horse is exceptionally long.

If the clot be examined microscopically, it is found to consist of fine fibrils, entangled in which are the blood-corpuscles; if the fibrin produced be washed completely free from blood, its appearance is well described by its name.

If the blood, instead of being allowed to clot spontaneously, be whipped with a rod or bunch of twigs, or, as we say, 'defibrinated,' the fibrin separates rapidly and coats the rod, while no coagulation in the remaining fluid can occur. The power of spontaneous clotting lies, then, in the production of fibrin.

These changes may be graphically represented thus:

On Clotting.

Blood.	Plasma.	Serum.	
		Fibrin.	Clot.
	Corpuscles.	Red.	
		White.	
		Blood platelets.	

When Whipped.

Blood.	Plasma.	Fibrin.	
		Serum.	Defibrinated blood.
	Corpuscles.	Red.	
		White.	
		Blood platelets.	

Fibrin is a yellowish-white, stringy-looking, bulky mass. Its bulky appearance would lead to the belief that it exists in blood in large quantities; it is found, however, to be by weight relatively small (0·2 to 0·4 per cent.).

The cause of coagulation has kept physiologists busy for many years, and even at the present time the matter has by no means been settled. The theory most generally accepted is that of Hammarsten—viz., that clotting is due to the conversion of a fluid fibrinogen into a solid fibrin, under the influence of a substance spoken of as fibrin ferment, which is described below.

If blood be prevented from coagulating, plasma can be obtained, and this plasma, depending upon the agents used in its production, will teach the main facts of coagulation. If it be obtained by cooling the blood, then the plasma will clot spontaneously if we allow the temperature to rise; if the plasma be obtained by previously mixing the blood with a definite amount of magnesium sulphate or common salt, clotting will occur on diluting it. If it be obtained by acting on blood with oxalates, then clotting can be brought about by the addition of a lime salt. The clot formed by the plasma coagulating is precisely the same as that formed by the blood coagulating; it is, of course, colourless.

If the above plasmas be acted upon by adding common salt to half saturation, a precipitate of **fibrinogen** occurs; this is a protein belonging to the globulin group, and has previously been alluded to. If this precipitate be redissolved by diluting the fluid, and allowed to stand, it clots spontaneously. If a solution of pure fibrinogen be prepared, it does not clot spontaneously, but it may be made to do so by the addition of a drop of serum or the washings of a blood-clot.

The substance which brings about coagulation of the blood is contained in the plasma; it is not found in the serum, as shown by the fact that the latter is incapable of spontaneous coagulation. The difference between plasma and serum, as we have already seen, is that the former contains fibrinogen and the latter does not.

Nor is clotting a function of the red cells, for lymph is capable of clotting, and there are no red cells in it; and, further, there is an abundance of red cells in defibrinated blood, yet clotting is impossible.

We have previously learnt that in the plasma both fibrinogen and serum-albumin are present; the proof that serum-albumin takes no share in the process of clotting is that, though serum contains an abundance of serum-albumin, yet spontaneous coagulation is impossible, nor can it be made to clot by the addition of such bodies as lead to clotting in a fibrinogen solution.

Everything points to the fluid fibrinogen of the plasma being converted into the solid substance fibrin, and in whatever other particulars physiologists differ regarding the question of coagulation, all are agreed on this fundamental fact. In the observations above described it has been shown that a solution of pure fibrinogen does not clot spontaneously, but that it at once coagulates on the addition of a drop of serum or washed blood-clot.

From this fact we learn that the conversion of fluid fibrinogen into solid fibrin cannot occur without the agency of another substance. The fibrinogen will not coagulate of itself; it requires to be rendered active by something contained in a drop of serum or a washed blood-clot. This substance is generally spoken of as **fibrin ferment**; its present-day name is **thrombin**. The term ‘ ferment ’ was employed since in some respects the substance resembled the class of bodies known as ‘ ferments,’ inasmuch as a very small amount appeared to be capable of acting on an indefinite amount of fibrinogen; it further resembled a ferment in its action, being closely dependent on temperature. It is now, however, more generally believed that a small amount of the ferment will not act upon an indefinite amount of fibrinogen, the amount of fibrin formed being proportional to the amount of ferment present.

It was stated above that a drop of serum added to a solution of fibrinogen at once causes clotting. Evidently, then, blood-serum contains in abundance the substance known as ‘ fibrin ferment ’ or ‘ thrombin.’ If the serum be boiled or heated to 65° C. (150° F.), a drop of it added to a solution of fibrinogen does not cause clotting; but this function can be restored by the addition to it of an alkali. This observation should largely, if not entirely, exclude thrombin from being classed as a ferment. A drop of stale serum will not produce clotting with fibrinogen. The reason why stale serum refuses to act is unknown.

Thrombin may readily be prepared by extracting a dried blood-clot with water. The addition of a few drops of this extract to hydrocele or pericardial fluid at once causes coagulation, for these fluids contain fibrinogen, but no ferment. Thrombin is a colloid, and its resistance to putrefaction suggests it is not a protein substance. According to some observers, thrombin is present in the circulating blood, but if blood be received with special precautions directly from an artery into a large bulk of alcohol, the clot, when dried and extracted as above, yields no thrombin. It seems reasonable to infer that as the blood does not coagulate in the vessels during life, there is no thrombin present. Nevertheless, if solutions of thrombin are injected into the circulation they do not produce intravascular clotting with the certainty that might be expected, and it has been suggested that in such cases the thrombin has been destroyed in the liver, but the evidence of this is not convincing. We shall look at the question again.

If thrombin does not exist as such in the blood-stream, to what is its origin to be attributed ? Blood received direct from the vessels into a solution of oxalate of soda will remain uncoagulated indefinitely, but the addition of calcium chloride at once causes clotting. This result was originally explained by saying that the lime in the blood was thrown out of solution by the oxalate, and that the addition of calcium caused coagulation. But an oxalate solution of fibrinogen is coagulated by an oxalate serum containing thrombin. Evidently, therefore, in the first of these two experiments thrombin was absent, and in some way or other was produced by the addition of calcium chloride. It is now supposed that the calcium is not concerned in the action of the thrombin on fibrinogen, but that its function is to assist in the production of thrombin from some antecedent substance. To this substance the name **pro-thrombin** or **thrombogen** has been given. According to some views, this substance exists in living blood, while others regard it as a product of the breaking down of the platelets and leucocytes of the blood after the latter has been shed.

If both thrombin and pro-thrombin are formed after the blood is shed, what is it that stimulates the production of pro-thrombin ? One view which finds many supporters is that the pro-thrombin is liberated from the disintegrating blood-cells by the action of a kinase,* **thrombokinase,** which, together with calcium salts, converts thrombogen into thrombin.

Another view is that the circulating plasma contains thrombogen, but not thrombokinase, the latter being liberated from the leucocytes and blood-platelets after shedding. In the presence of calcium, thrombokinase converts thrombogen into thrombin.

Not only is thrombokinase present in the above cellular elements of the blood, but it exists in all the tissues of the body.

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* *Kinases* are activating substances.

The practical importance in the case of a wound of having thrombokinase at hand to act on the thrombogen, and so cause coagulation by the production of thrombin, is very evident, for the cessation of hæmorrhage is due to the formation of fibrin in the mouths of the vessels.

There is a substance known as 'nucleo-protein,' readily obtained from tissue-cells, thymus, kidney, lymphatic glands, and other organs, which is very closely identified with thrombin. If nucleo-protein be prepared, and a large dose injected into the veins of an animal, intravascular clotting and death at once occur. On the other hand, if small doses be injected at intervals, no such effect is produced—in fact, the blood is rendered uncoagulable. To this phenomenon the term 'negative phase' has been applied, in contradistinction to the positive phase in which clotting at once occurs. The explanation which has been offered of the negative phase is that an *antibody* is produced which neutralises the thrombokinase. But it has also been held that two different substances are obtainable from the above tissue-cells—one, *leuconuclein*, which accelerates, and the other, *histon*, which retards coagulation; whichever effect is observed is said to depend upon the relative amount of each present.

The view that an antibody exists in living blood which prevents coagulation in the vessels is urged by some. Such an antithrombin has not at present been extracted from the inner wall of the bloodvessels, but the theory offers an explanation, not only of why blood remains fluid during life, but also of the fact that coagulation of the blood in the vessels after death is a slow process. It also offers a reasonable explanation of a very old experiment on the horse, in which the jugular vein, after being occluded by ligatures and excised, maintains the enclosed blood in a fluid condition for one or two days, so long as it is left in contact with the wall of the vessel; clotting, nevertheless, at once occurs on removal. Fig. 8 shows diagrammatically this so-called 'living test-tube' experiment, the explanation of which was for years attributed to the influence exerted in some way or other by the normal endothelium of the vessel on the contained blood.

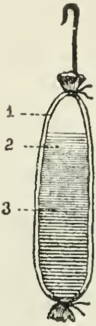

Fig. 8.—Vein of a Horse tied between Two Ligatures.

1, Plasma; 2, white corpuscles; 3, red corpuscles.

Intravascular clotting may occur under pathological conditions, as when the inner coat of the bloodvessel is injured, and the cells then act as a foreign body. This may be seen in a ligatured vessel, while pathologically the horse provides a classical example in the injury occurring to the iliac arteries, which leads to thrombosis.

Circumstances influencing Coagulation.—Clotting in shed blood may be retarded or hastened by certain conditions. The blood of a horse received into a vessel so constructed as to expose it to a *freezing temperature* may be kept fluid for an indefinite period, though coagulation will at once occur when the temperature is allowed to rise. The probable explanation of the phenomenon is that the low temperature keeps the corpuscles from disintegrating.

Clotting is delayed by the addition to the blood of certain *neutral salts* of the alkalies and alkaline earths; the best salt to employ for the purpose is magnesium sulphate. The plasma so obtained is spoken of as salted plasma, and is largely used in physiological experiments on the blood. It is not known how neutral salts prevent coagulation; it may be by keeping the corpuscles intact, or by inhibiting the conversion of pro-thrombin to thrombin. The addition of dilute *acetic acid* or the passage of a current of *carbonic acid gas* through blood prevents coagulation by precipitating fibrinogen. The addition to blood of a weak solution of *potassium* or *sodium oxalate* prevents clotting by combining with the lime in the blood. Without the presence of calcium, thrombogen cannot, as we have seen, become converted into thrombin; if, however, a soluble calcium salt be added, the power of clotting is restored. *Sodium fluoride* has much the same effect on blood as sodium oxalate; it combines with the lime; but the power of clotting is not restored by merely adding a soluble calcium salt. Some tissue extract must also be included, for the fluoride has interfered with the formation of the thrombokinase.

The action of certain *organic substances* in retarding blood-clotting is very remarkable. If *peptone* be injected into the blood of a dog, such blood will not clot; it can be shown that this is not directly due to the action of the peptone, for the latter may be added to blood without inhibiting coagulation. Peptone introduced into the circulation causes the secretion in the liver of a substance which prevents blood-clotting, an antithrombin. *Leech extract* contains a similar substance. This antithrombin—designated *hirudin*—is secreted by the salivary glands of the leech. When an extract of these is injected into the circulation, the blood loses its power of clotting, and, unlike peptone, leech extract, when added to blood drawn from the body, prevents coagulation. The bleeding following leech-bites and the fluid condition of the blood in the body of the leech are due to the action of this antithrombin.

Clotting of blood is retarded if the fluid as shed is received into a vessel the wall of which is thinly coated with oil. The shape of the collecting vessel has also an influence over coagulation, clotting being much slower in a deep, smooth vessel than in a rough, shallow one. By increasing the foreign surface to which the blood is exposed clotting is hastened. This is the explanation of the effect of washing a bleeding wound, while the application of compresses influences in some way or other the formation of thrombin.

The **Extractives** of the blood are fats, cholesterin, lecithin, creatine, urea, hippuric acid, uric acid, and grape-sugar, all in small and varying quantities. The amount of fat in the blood during digestion is 0·4 to 0·6 per cent.; in dogs fed on a fatty diet it may reach 1·25 per cent., and may give the serum a milky appearance. There is twice as much fat in the serum of recently-fed horses as in the serum of those kept starving. Other extractives such as soaps are found to the extent of 0·05 to 0·1 per cent.; urea, 0·02 to 0·04 per cent.; sugar, 0·1 to 0·15 per cent. The corpuscles contain neither sugar nor fat, and possess a larger amount of cholesterin and lecithin than the plasma.

The characteristic **Difference between Arterial and Venous Blood** is that the former contains more oxygen and less carbonic acid than the latter, though there is always, in fully arterialised blood, about twice as much carbon dioxide as there is oxygen (see p. 123). Arterial blood also contains more water, fibrinogen, extractives, salts, and sugar, fewer blood-corpuscles, and less urea; its temperature is, on the average, 1° C. lower. The dark colour of venous blood is not due to the greater amount of CO_2 it contains, but to the diminution of oxygen in the red blood-cells. The alteration in colour effected by the addition of reagents and gases to blood is probably due partly to alterations in the shape of the corpuscles themselves, which become more concave on the addition of oxygen and less concave on its removal, but mainly to the fact that oxyhæmoglobin is brighter in colour than hæmoglobin.

The **Salts** of the blood are divided between the plasma and the corpuscles. The distribution of these is not the same in all animals; in the horse and pig, for example, sodium exists only in the plasma, there being none in the corpuscles, while in both animals the potassium in the corpuscles is very high; in the ox and dog both corpuscles and plasma contain sodium. Sodium chloride is the most abundant salt of the blood, potassium chloride and sodium carbonate come next, and lastly phosphates of calcium, magnesium, and sodium. The chief inorganic substance of the cells is potassium phosphate. The following table from Bunge bears on the question of the salts of the blood in different animals:

	1,000 grammes of corpuscles contain—			1,000 grammes of serum contain—		
	K.	Na.	Cl.	K.	Na.	Cl.
Horse -	4·920	0	1·930	0·27	4·43	3·750
Ox -	0·747	2·093	1·635	0·254	4·351	3·717
Pig -	5·543	0	1·504	0·273	4·272	3·611

Water free from salts is destructive to protoplasm; no doubt, therefore, one important function of the salts in the blood is to maintain the vitality of the tissues by preserving the osmotic equilibrium. Sodium chloride is here especially valuable, and its extensive presence in blood (60 per cent. to 90 per cent. of the total amount of ash) corresponds to its importance. As the blood is simply the carrier of the salts, and the only channel by which the tissues can obtain them, it by no means follows that all the mineral matter found in it is essential to its own repair and constitution.

The **Temperature of the Blood** in the different domestic animals varies from 37·8° C. to 40·54° C. (100° to 105° F.), the warmest blood in the body being found in the hepatic veins.

The **Quantity of Blood in the Body** cannot be determined by mere direct bleeding alone. After all the blood is drained off, the vessels require to be washed out, and the quantity of blood in the water estimated by the colour present; the body has then to be minced and macerated, and the quantity of blood in the resulting fluid estimated by the colour test, comparison being made with a standard solution of blood.

By Haldane and Lorrain Smith's carbon monoxide process the amount of blood in the living animal may be calculated. The essential steps in this process are to estimate first colorimetrically the percentage of hæmoglobin in the blood, and then the extent to which this is saturated by breathing a measured volume of carbon monoxide. In this way the total capacity of the blood for carbon monoxide may be ascertained, and the carbon monoxide capacity being the same as the oxygen capacity, the volume of the blood may be readily calculated.

Sussdorf* puts the proportion which the weight of the blood bears to the body weight as follows:

Horse - $\frac{1}{15}$ = 6·6 per cent. of the body weight.
Ox - $\frac{1}{13}$ = 7·71 ,, ,, ,,
Sheep - $\frac{1}{12}$ = 8·01 ,, ,, ,,
Pig - $\frac{1}{22}$ = 4·6 ,, ,, ,,
Dog - $\frac{1}{11}$ to $\frac{1}{18}$ = 5·5 to 9·1 per cent. of the body weight.

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* Ellenberger's 'Physiologie der Haussäugethiere.'

The same observer gives the amount of blood in the body of the horse at 29 litres (66 pounds, or nearly 50 pints).

The **Distribution of Blood in the Body** (Fig. 9) is believed to be as follows:

About one-fourth in the heart, lungs, large vessels, and veins.
,, ,, liver.
,, ,, skeletal muscles.
,, ,, other organs.

It is probable that in the horse the liver would contain less than one-fourth the bulk of blood, while the skeletal muscles would contain more. Under certain conditions the abdominal veins are capable of containing the whole of the blood in the body. When an organ is active it receives more blood than when in a state of rest; this increase has been variously estimated at from 30 to 50 per cent.

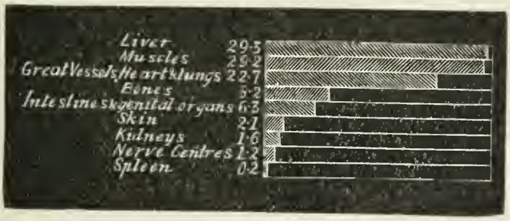

Fig. 9.—Diagram to illustrate the Distribution of the Blood in the Various Organs of a Rabbit, after Ranke's Measurements (Stewart).

The numbers are percentages of the total blood.

Regeneration of the Blood after Hæmorrhage.—Regeneration of the fluid portions of the blood is extremely rapid, experiments showing that after slight hæmorrhage the normal volume is regained within a few hours, and after severe hæmorrhage in from twenty-four to forty-eight hours. This is supported by clinical observation; in the days of severe bleedings venesection to the extent of producing syncope was frequent, yet in a very short time the volume was restored. In these cases it is the plasma which is rapidly replaced. The red cells and hæmoglobin take longer to prepare, probably several days, perhaps even two or three weeks. In the dog exact observation shows that a hæmorrhage of from 2 to 3 per cent. of the body weight is readily recovered from, while a loss of 4·5 per cent., which represents half the blood in the body, is generally fatal. Percivall tells us* that in the horse he occasionally drew 3 gallons of blood, which may be taken as half the amount in the body, apparently without fatal consequences.

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* 'Hippopathology,' vol. i., p. 95.

Transfusion of warm normal or physiological saline solution (NaCl 0·9 per cent.) is capable of keeping the heart beating even after severe hæmorrhage, showing that the immediate essential factor is the restoration of bulk to the empty vascular system. In order that the blood-pressure should be kept up after saline transfusion, the addition of gum to the fluid is necessary (Bayliss). Transfusion of blood is not without danger, for, as has been shown in dealing with hæmolysis, the serum of one animal may be toxic to another.

The **Gases of the Blood** are more conveniently dealt with in the chapter on Respiration (see p. 123).

Composition of the Blood.—Reviewing the various analyses which have been published of the blood of animals, the following represents the average composition of the fluid:

The Plasma.

Water	90 parts per cent.
Proteins	8 or 9 parts.
Fats	0·1 part.
Extractives	0·4 ,,
Salts	0·8 ,,

The Corpuscles.

These represent from one-third to half the weight of the blood, and consist of—

Water	64 parts per cent.	
Solids	35 ,,	consisting of 32 per cent. hæmoglobin, 0·1 per cent. proteins.
Salts	1 part.	

Taking the blood as a whole, the following represents approximately its composition in every 100 parts:

Water	81 parts.		
Solids	19 ,,	Hæmoglobin	13 parts.
		Proteins	4 ,,
		Salts	1 ,,
		Extractives	0·6 ,,

The Blood in Disease.—The blood plays two distinct parts in disease; it is a carrier and distributer of infection to the body-cells, and, further, it may itself undergo profound pathological change.

All the specific infective diseases of animals are spread through the body by means of the blood-stream. It is true that the initial source of entry may be an allied passage—the lymph-stream—but it is by means of the blood that the final and complete invasion of the body is effected. Nor does this observation apply to specific diseases only; if we take two such opposite conditions as anthrax and poisoning by arsenic, it is the blood in each case which is responsible for the distribution of the infecting agent.

The blood-tissue itself may be the seat of disease; micro-organisms may live and multiply in the plasma, and infect the whole body as in anthrax. Some of the organisms may be so small as to be ultramicroscopic, and it should be remarked that some of the most acute and fatal infectious diseases of animals are caused by organisms of this class—for example, rinderpest, foot and mouth disease, rabies, and African 'horse sickness.' And, in spite of the fact that these microbes have not been seen, their existence is undoubted, the best evidence of which is that some of them are sufficiently large to be caught in the pores of a filter, leaving the filtrate sterile. Other organisms attack the blood-cells, either from without or within—for example, the important group of Trypanosomes, the malaria parasite, the organism of Texas fever, and suchlike. In these cases the product of red-cell destruction may show itself by the discoloured urine, and is evident in the tissues—for instance, the liver and spleen.

Compared with the red corpuscles, the white are seldom affected with disease, but there are certain pathological conditions associated with a great increase in their number (*leucocytosis*), and others in which the white cells are reduced in number (*leucopænia*).

There are other conditions affecting the blood—for instance, *Purpura*—which cannot be attributed to parasitic agency. In this disease, either from defects in the blood or vessel-wall, hæmorrhage takes place into the tissues. No organ appears to be able to escape, though probably the subcutaneous and muscular tissues are the most frequent seat of the hæmorrhage.

Quite as strange and obscure is the dietetic disease of equines known as *hæmoglobinuria*, in which the animal in the middle of work suddenly falls paralysed; the urine becomes coffee-coloured and loaded with methæmoglobin, in consequence of the destruction of the red cells. What the destructive agent is, is at present unknown, but it is probably one of the poisonous products of protein disintegration, which will be found dealt with in the chapter on Digestion.

Blood-letting in the treatment of disease was at one time so universal that it came to be regarded as the 'sheet-anchor' of life, and animals were regularly bled in *order to keep them in health.* 'Blood-letting' was killed by abuse; it is now a question whether the pendulum has not travelled too far in the other direction, and the employment of a physiological means in the treatment of disease been too long neglected. Towards the end of the eighteenth century a full blood-letting for the horse was from 4 to 5 pints. During the first half of the nineteenth century 8 pints were considered a moderate bleeding. Under pressure of acute disease 3 gallons were drawn, and Percivall tells us he had heard of 4 gallons being taken (see p. 27).

This is the abuse we allude to as having caused the fashion to change. Such heavy blood-lettings must have been responsible for considerable mortality. Percivall describes the 'impression on the system,' which was considered a certain indication if blood-letting was to prove beneficial. As the pulse began to sink, the horse became very uneasy, jerking the head up and down, moving backwards until finding support for the hind-quarters; respirations increased, deep sighing followed, the body rocking from side to side, in danger of falling headlong; shivering; and, after the operation, sweating. A second and even third bleeding was employed.

The efficacy of bleeding healthy animals to improve nutrition was fully accepted, and Percivall declares his opinion that, if persisted in, it became necessary for preserving health. An increased disposition to fatten was observed in young animals submitted to moderate bleeding, and farmers employed this knowledge regularly in fattening their young stock.

CHAPTER II

THE HEART

The blood in the body has to be kept in constant motion, so that the tissues which depend upon it for their oxygen may be continuously supplied, and also that the blood when rendered impure by the changes in the tissues may be rapidly and effectually conveyed to those organs where its purification is carried out.

The heart is the organ which pumps the blood over the body, not only distributing it to the tissues, but forcing it on from these back to the heart again, to be prepared for redistribution. It may be described as a hollow muscle divided into two compartments, usually known as right and left, but in quadrupeds really anterior and posterior, each compartment being divided into an upper half or auricle and a lower or ventricle. Opening into the auricles are large veins which convey the blood back to the heart, while from the ventricles other vessels, arteries, take their origin for the conveyance of blood from the heart. The auricles and ventricles are separated by a valvular arrangement, and the two sides of the heart are separated by a muscular partition (Fig. 10).

Thus far the general arrangement of both right and left sides is much the same, each having to receive and then to get rid of a certain quantity of blood received by it. But the blood sent into the right side of the heart is very different from that received by the left, and with this difference we must for a moment deal. The whole of the impure or venous blood in the body is brought into the right side of the heart for the purpose of being distributed to the lungs, where it is purified; this arterial or purified blood is brought back from the lungs into the left heart for distribution to the body. The passage of the impure or venous blood from the right side of the heart through the lungs to the left side is known as the *Pulmonic* circulation, that of the blood, thus purified, through the body back to the right side of the heart is called the *Systemic* circulation (Fig. 11).

Mention has been made of *valves* in the cavities of the heart; they are found on both sides separating auricle from ventricle, and are known as the right auriculo-ventricular or tricuspid valve, and the left auriculo-ventricular or mitral valve. In addition to these, valves are found in the vessels arising from the ventricles—viz., in the pulmonary artery and the aorta; these valves, pulmonary and aortic, are known as the semilunar valves. No valves are found guarding the entrance of the vessels (veins) into the auricles. In order to understand the function of these valves, which play such an important part in the physiology of the heart, it is necessary that we should briefly detail the course which the blood takes from the time it enters the right auricle until it completes the round of the circulation and finds itself at this auricle again.

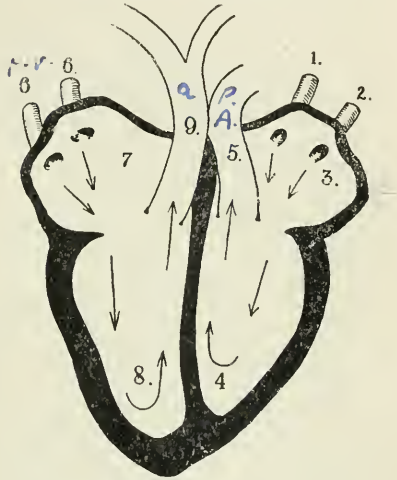

Fig. 10.—Diagram of the Circulation through the Heart.

1 and 2, The venæ cavæ; 3, right auricle; 4, right ventricle; 5, pulmonary artery; 6, 6, pulmonary veins; 7, left auricle; 8, left ventricle; 9, aorta dividing into anterior or posterior. The arrows represent the direction taken by the blood-stream.

Course of the Circulation.—The venous blood from the whole of the body flows into the right auricle by means of the anterior and posterior venæ cavæ; it then passes through the tricuspid valve into the right ventricle; from the right ventricle it travels to the lungs by means of the pulmonary artery, where, having been exposed to the action of the air and become greatly changed in its gaseous composition, it returns to the heart as pure blood by means of the pulmonary veins, pouring itself into the left auricle. The blood now passes through the auriculo-ventricular opening into the left ventricle, and thence into the aorta to be pumped all over the body, being distributed by means of the arteries and capillaries; it is then collected by the veins, and eventually brought back to the heart to undergo afresh its distribution to the lungs and body (Fig. 11).

The use of the valves is to allow of and to insure the transference of blood from auricles to ventricles, and from the ventricles to the aorta and pulmonary artery without any chance of regurgitation. This they do in virtue of the fact that they are so constructed and arranged as to open only in that direction towards which the blood has to be sent.

Position of the Heart.—The heart occupies a position in the middle line of the chest, and is suspended from the spine by means of its arterial trunks. These are its only means of support. Some assistance may be afforded by its connection with the root of the lungs; but in thinking of the heart as a pump we must remember that all the movements it executes in its constant work are carried out as the organ literally hangs from the spine. It rests on nothing; the apex is clear of the sternum; the pericardium keeps it in its place, but is no mechanical aid to keeping it in position. In the dog the pericardium obtains attachment to the diaphragm, but not in the horse and ruminants. Further, in the dog and cat the heart rests on the upper face of the sternum, whereas in the horse it does not touch the sternum. Fig. 12, or better still Fig. 45, gives an accurate notion of the position of the heart. It will be observed that the organ is tilted forward, the base lying in front of the apex.

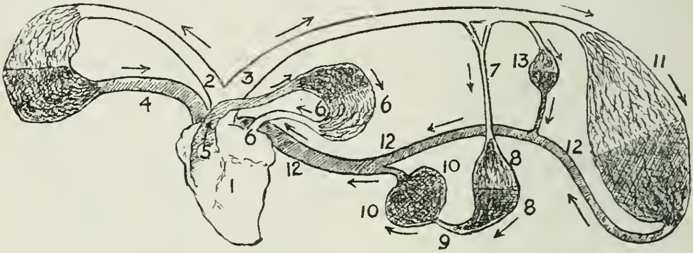

Fig. 11.—Diagram of the Circulation of the Blood.

1, The heart; 2, anterior; 3, posterior aorta; 4, anterior vena cava; 5, pulmonary artery; 6, pulmonary veins; 7, mesenteric arteries; 8, intestinal capillaries; 9, portal vein; 10, the liver, the veins from which open into (12) the posterior vena cava; 11, the circulation through the hind extremities; 13, the circulation through the kidney.

The base of the heart is uppermost, and the organ in the horse occupies a position opposite to the third, fourth, fifth, and sixth ribs. It is between the fifth and sixth ribs, just above their sternal insertion, that the impulse of the heart can be felt. On its right face is the right lung, and on its left, part of the left lung, the big triangular notch in which exposes the left ventricle and enables it to make its impulse felt against the chest-wall. The anterior part of the heart is formed by the right auricle and ventricle, the posterior by the left auricle and ventricle. The pulmonary artery runs along the left face, and the posterior vena cava lies on the right face.

Heart Muscle.—The heart muscle in structure is considered to come midway between skeletal and involuntary muscle. Until recently its fibres were described as short, branching, anastomosing, and possessing no sarcolemma. There is good reason to believe that this account is no longer correct, and that the fibres, instead of being short, form a continuous sheet, fibrils passing from fibre to fibre, and so constituting an anastomosis in every direction. There is evidence also that a sarcolemma is present, though it is delicate in structure. The fibrils, or sarcostyles, of which the fibres are composed, are both longitudinally and transversely striated.

Fibres, described as the *fibres of Purkinje,* are found beneath the endocardium of the horse, ox, and sheep. They give a greyish appearance to the part, and on microscopical examination are found to consist of large polyhedral, clear cells, containing granular substance, and one or more nuclei. These fibres are connected with a peculiar band of muscle which forms a connection between the auricle and ventricle. This band or bundle is known as the **Auriculo-ventricular** or **A.V. Bundle,** and is the discovery of Kent and His. Originally it was held that the muscular structure of the auricle and ventricle was distinct, the chambers being separated by a fibrous ring; but in the hearts of the ox and sheep this bundle of muscle connecting the auricles with the ventricles can easily be traced by its paleness. It is found in all mammalian hearts. In the mammalian heart there are two small masses of so-called 'nodal' tissue, intermediate between muscle and nerve in structure—namely, the sinu-auricular and the auriculo-ventricular nodes (Keith and Flack). The former is situated at the junction of the superior vena cava and right auricle, and the latter at the base of the inter-auricular septum on the right side below and to the right of the coronary sinus. These nodes are connected with one another

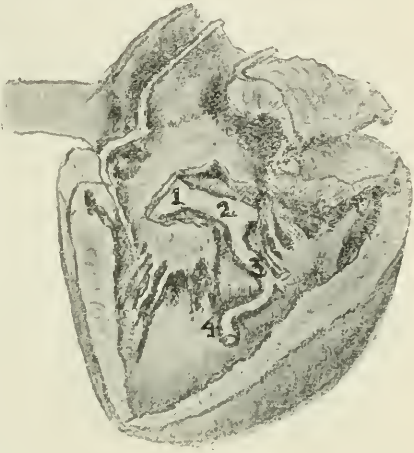

FIG. 12.—RIGHT AURICLE AND VENTRICLE OF CALF, TO SHOW AURICULO-VENTRICULAR BAND (AFTER KEITH).

1, Auriculo-ventricular (A.V.) node; 2, main auriculo-ventricular bundle; 3, right septal division of the bundle; 4, moderator band.

through the interauricular septum, and the S.A. node, which may be regarded as the pace-maker of the heart, is in intimate connection with the cardiac nerves. From the A.V. node, Fig. 12 (1) is given off the main bundle (2); this divides into right and left divisions, one running to the right ventricle, the other to the left. The right heart bundle (3) runs downwards into the ventricular septum, and is distributed to the *musculi papillares* and moderator bands. In the left heart the bundle reaches the left ventricle from the right auricle; it then runs down the ventricular septum, and, like its fellow in the opposite side of the heart, is distributed to the *musculi papillares* and moderator bands.

The **muscular walls of the auricle and ventricle** are constructed of layers of red fibres, varying greatly in thickness and of extremely complex disposition, especially around the ventricular cavities. The ventricular walls are thicker than those of the auricles, and the left side of both cavities is better developed than the right. In certain portions of the right auricle the wall is so thin as to be semi-transparent, and appears, in fact, to consist of little else than the two layers of serous membrane which cover and line the heart. The ventricular walls are of unequal thickness; at the apex of the heart they are reduced to a few fibres of muscular tissue one-eighth of an inch in thickness. Chauveau, in fact, says that at this point there is nothing more than two layers of serous membrane—viz., that lining and that covering the heart.

The varying thickness of the walls of the heart is due to the complex arrangement of the various layers of fibres; these may, broadly speaking, be divided into two main groups—an internal, belonging to each auricle and each ventricle separately, and an external, belonging to both auricles and both ventricles. Excluding the A.V. bundle just described, the fibres of the auricles are confined to the auricles, and the fibres of the ventricles to the ventricles; the advantage gained by this arrangement is obviously connected with the independent contraction of auricles and ventricles.

The muscular layer peculiar to each ventricle is very complex, but, generally speaking, may be described as a scroll of fibres of several layers running obliquely around each ventricle, and where the scrolls meet forming the ventricular septum. The scrolls are attached above to the auriculo-ventricular ring, but are left open below. If we can imagine these scrolls separated from the other muscle of the heart, they would present the appearance of a pair of hollow cones. Covering this internal layer is an external, belonging in this case to both ventricles; it takes its origin from the auriculo-ventricular ring, and describes a spiral course in descending from base to apex of the heart, where the fibres form what Henle described as a vortex (Fig. 13); they then pass upwards through the opening in the scrolls of the inner layer, and so gain the interior of the ventricles. Some of the fibres pass to the *columnæ carneæ*, others to the *musculi papillares*, while the majority gain insertion into the auriculo-ventricular ring from which they had their origin. As pointed out by Chauveau, whose account of the arrangement of the fibres in the heart of the horse we have mainly followed, this layer forms between its origin and insertion figure of eight loops, the smallest loop being at the apex of the heart, where at its centre it leaves a very small space, through which a probe may be passed into the ventricle without piercing anything but the external and internal layer of serous membrane.

The fibres of the auricle are much simpler in their arrangement. Those peculiar to each cavity are disposed in several fasciculi, some circular, especially those surrounding the mouths of the vessels, others, in the general body of the auricle, in interwoven loops. The septum is formed where the two sets proper to each auricle meet. The fibres common to both auricles are generally arranged transversely.

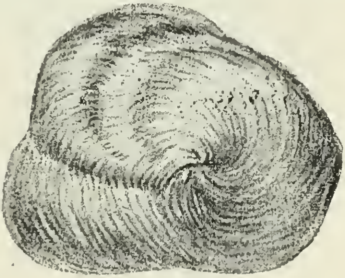

Fig. 13.—Apex of Heart, showing Vortex Arrangement of Fibres (after Krause).

It may be added that anatomists are not agreed as to the arrangement of the fibres of the heart muscle, and this may to some extent be due to the fact that the system is not the same in all animals.

The arrangement just outlined has, however, this advantage, that it certainly appears to provide for the squeezing and wringing movement to which the ventricular contents are exposed, the shortening of the heart wall from base to apex, and the contraction of the *musculi papillares* at the moment the valves close. Far simpler is the disposition of the muscular fibres of the auricles; physiologically these cavities have been regarded as the dilated extremity of the vessels entering the heart, and their function as more that of a well than of a pump. Nevertheless, the existence of a network of muscular pillars in the auricles, especially the dense bands in the left, warn us to be careful not to regard these cavities in the horse as mere passive channels of the circulation. Keith dismisses the reservoir theory of the auricles as being opposed to their structure and describes them as loading pumps for the ventricles.

Keith* further points out that the muscular walls of the heart must have some fulcrum from which to act. The auricles are fixed by means of the pericardium to the lungs and walls of the thoracic cavity, and a point from which they can act is thus obtained. When the ventricles contract, the base of the aorta, where it arises from the left ventricle, becomes a fulcrum. Nevertheless, we know that in some animals the heart will continue to contract rhythmically for some time after removal from the body, even when the above-mentioned fulcra are detached. There are certain fibrous rings found in the heart where the valves are situated to which these and the muscular fibres obtain a firm attachment. The ring surrounding the aortic opening in the ox has in its substance one or more pieces of bony tissue, and this is also common in the horse.

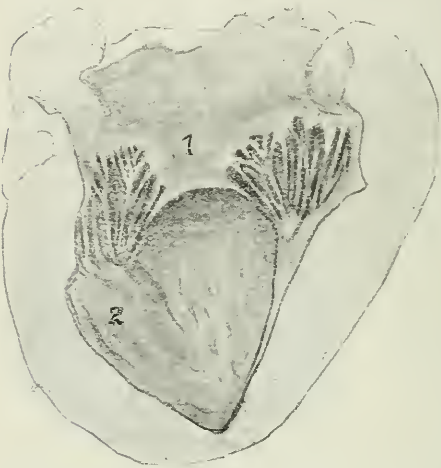

Fig. 14.—Left Ventricle of Horse exposed to show Mitral Valve.

1, Portion of valve; 2, *columnæ carneæ*, on the upper surface of which are found the *musculi papillares*, to which the *chordæ tendineæ* are attached.

The cavities of the heart are lined by the endocardium, which is reflected over the valves; this membrane in the left auricle of the horse is of a peculiar grey colour, due to the fibres of Purkinje.

Valves of the Heart.—The *auriculo-ventricular* valves are made up of fibrous membrane, in which a small proportion of muscular fibre is found close to the attached border. The *mitral* or *bicuspid* valve in the horse consists of one large distinct segment, and several smaller ones united to form a second; the tricuspid consists of three segments, one, much larger than the others, being placed opposite to that portion of the ventricle which leads to the pulmonary artery.

The free edges of all the valves are held in position by large and small tendinous cords (*chordæ tendineæ*) composed of fibrous tissue, which are inserted into *musculi papillares* found on the internal surface of the ventricle; the cords from one papilla do not all pass to one segment of the valve, but to all (Fig. 14).

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* 'The Functional Anatomy of the Heart,' Professor Arthur Keith M.D., F.R.S., *British Medical Journal*, March 30, 1918.

The function of the papillæ is to restrain the valves from being forced too far into the auricle during the contraction of the ventricle, and this they accomplish by gradually shortening as the walls of the ventricle approximate, and thus exerting traction on the cords (Fig. 15). This shortening is brought about by the layer of muscular fibres which at the apex passes from the external face of the heart into the interior of the ventricles, and thence to the fleshy columns and papillary muscles (p. 35). Other bands pass from one side of the ventricle to the opposite wall; they are called *moderator bands*, and their function is to protect the ventricular wall from undue distension.

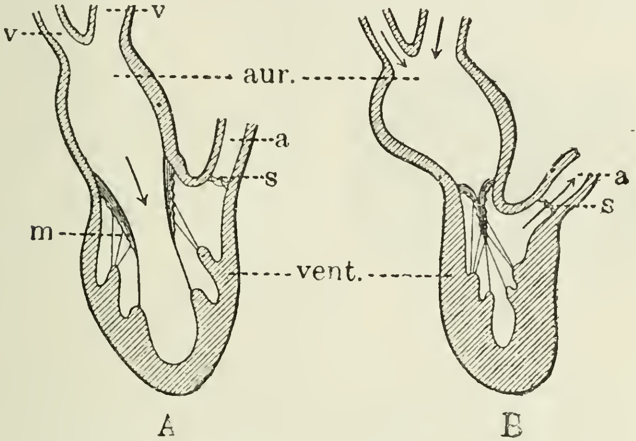

Fig. 15.—Diagram to illustrate the Action of the Valves of the Heart (Huxley).

In A the auricle is contracting, ventricle dilated, mitral valve open, semilunar valves closed. In B the auricle is dilated, ventricle contracting, mitral valve closed, semilunar valves open. *Aur.*, auricle; *vent.*, ventricle; *v.*, *v.*, vein; *a.*, aorta; *m.*, mitral valve; *s.*, semilunar valve. Note the manner in which the papillæ have shortened in B, in order to compensate for the approximation of the ventricular walls to the surfaces of the mitral valve.

The valvular flaps meet in the most perfect apposition when the ventricles contract; their edges are inverted, and the sides of the valves curl in and lie so close to their fellows that nothing can escape upwards into the auricles (Fig. 16). This may be readily demonstrated in the dead heart if one ties the aorta and pulmonary veins, and introduces into the left auricle a tube which admits a powerful jet of water; the left side of the heart distends and hardens, and at last water forces its way out of the hole in the auricle through which the tube is inserted. If the auricle be now opened, the ventricle is found cut off from view by a tense, membranous, parachute-like dome, convex towards the auricle, which is the mitral valve in position; not a drop of water will escape from the ventricle, though the heart be turned upside down, and it requires some little force to depress the valve.

During the filling of the ventricle the auriculo-ventricular valves are coming into position; the blood is under them, and the final systole of the auricle, by raising the pressure in the ventricles, forces these valves into their place, and bulges them upwards towards the auricular cavity. We have seen that even in the dead heart their fit is so perfect that they render the ventricle water-tight. But in the living heart the walls of the ventricles are approximating as they contract on their contents, and though the internal diameter is being reduced in every direction, this does not disturb the accuracy with which the valves apply themselves to each other. The papillary muscles compensate for the approximation of the ventricular walls by constantly shortening, and through the *chordæ tendineæ* maintain the segments of the valves in apposition and prevent further encroachment on the auricle.

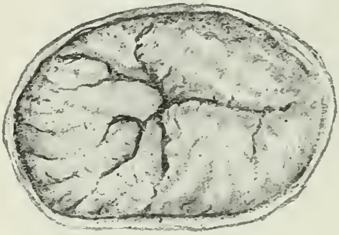

FIG. 16.—TRICUSPID VALVE OF THE HORSE IN CLOSED POSITION SEEN FROM THE AURICLE.

Note the cracks in the surface, which show where the margins of the valves meet, and fold in against each other like the lips of a toothless mouth.

The *semilunar* or *sigmoid valves*, which guard the entrances of the aorta and pulmonary artery, are composed of fibrous tissue, and possess at the centre of each segment a small hard body, the *corpus Arantii*, which is particularly well marked in the aortic valves. It is generally supposed that these shot-like bodies complete the central sealing when the valves are closed, but this view gives too little attention to the fact that the valves not only meet at their free border, but overlap. Chauveau states that, with his finger in the pulmonary artery of the horse, he has tried to hold back one flap in order to keep the opening patent, but the two remaining segments applied themselves so closely to his finger that the orifice was closed. That these bodies are additional aids to the closing of the valves completely tight is undoubted, but the overlapping of the valves is the more important factor.

When the sigmoid valves are not in action, they still stand out in the blood-stream, and do not lie against the wall of the vessels, as was at one time supposed, nor do those in the aorta cover the opening of the coronary arteries. It is probable that the valves are enabled to stand out in the blood-stream through the action of vortex currents, and while thus waiting for their turn in the heart's cycle they form a triangular orifice with curved sides.

It is generally believed that both the aortic and pulmonary valves are closed by the regurgitation of the blood; but it has been pointed out that the blood, as it is leaving both ventricles, is streaming through orifices which at that time are mere chinks, owing to the pads of heart muscle which take their origin from all sides of the mouths of the vessels. Vortices are thus created in the space between the arterial root and the edge of the valves. These vortices tend to press the edges of the valves together, and the valves consequently close the moment the blood actually ceases to stream through the narrow crevice. In this way there is no regurgitation, as the valves are closed before the recoil of the aorta. If this explanation be correct, the second sound of the heart must be considered due to the sudden *tension,* and not to the closure, of the aortic valves at the time of the aortic recoil.

It is of the utmost importance to bear in mind that the force of the aortic reflex is not expended wholly on the valves, but largely on the muscular tissue of the ventricle, which here, as the result of the orifice contracting, forms a large circular pad. In order to permit this strain to fall on the heart wall itself, the diameter of the aorta is much greater than the opening out of the ventricle.

Movements of the Heart.—If the exposed mammalian heart be watched at work, a great deal may be learnt of its action. It will be observed that both auricles contract together and both ventricles together; further, that certain changes in shape occur. The contraction either of auricle or of ventricle is spoken of as its **systole,** while the subsequent relaxation is described as its **diastole.** The contraction of the ventricles is succeeded by a *pause,* during which the heart is in a state of relaxation.

A **Cardiac Cycle** is the term used to describe the changes which occur in the heart during the time which elapses between one contraction or relaxation of the auricle, and the one which immediately succeeds it.

We may take the moment when the blood is entering the auricles from the venæ cavæ and pulmonary veins as the most convenient point to start from. This flow is brought about by the pressure of blood in the veins, which, though low, is yet higher than that in the auricles. The influence of gravity is also a great aid to the filling of the auricles, for, speaking broadly, excepting in the limbs, the greatest number of the veins in the body of quadrupeds is above the heart. The emptying of the anterior and posterior venæ cavæ is largely assisted by gravity; even in the latter there is a downward incline in the vessel from the last valves met with in the iliac veins to the right auricle. Besides the influence of gravity there is the contraction of the abdominal wall and consequent pressure on the viscera to be considered, so that at each expiration the blood is spurted along the posterior vena cava towards the auricle. Finally, there is an aspiration in the veins produced by the auricle, and caused by a relaxation of its walls after the previous contraction. There is also an aspiration in the thorax, the result of inspiration, which produces a negative pressure in the veins leading to the heart, and so draws blood towards the heart from the veins lying outside the thorax.

By a combination of these means the auricles are filled with blood, and a wave of contraction which first appears at the vessels leading into them passes over the chambers; the auricular appendage becomes pale, the auriculo-ventricular groove is drawn upwards, and the auricles, by a sudden sharp and brief contraction, empty their contents into the ventricles. At this moment there is a backward positive wave produced in the anterior vena cava, which shows itself by a pulsation in the jugular veins at the root of the neck, well seen in the horse.

The effect of the auricular contraction is to complete the filling of the ventricles and to close the valves by raising the pressure in those cavities. During the whole time the valves are open the ventricle is filling; what the systole of the auricle effects is the final filling of the ventricle. The auriculo-ventricular valves, which during the filling have been gradually coming into position, are now, under the sudden increase of intraventricular pressure, rapidly closed, and bulge into the auricle, their closure contributing to the production of the first sound of the heart. The valves are prevented from going too far by the *chordæ tendineæ*, which are acted upon by the gradually contracting *musculi papillares*, as previously explained. At this moment the blood imprisoned in the ventricles is shut off from the auricles by the closed auriculo-ventricular valves, and shut off from the aorta and pulmonary artery by the closed semilunar valves. The ventricles now contract and raise the pressure within their cavities in order to force open the semilunar valves, for until the pressure within the ventricle exceeds that in the aorta and pulmonary artery these two avenues of escape are closed. While the intraventricular pressure is being increased by the walls contracting tighter and tighter on the imprisoned blood, the heart is changing in shape; it is becoming more globular, its walls are growing tenser, it is shortening from base to apex, and in its writhing, screwing efforts to overcome the pressure in the aorta and pulmonary artery it is twisting slightly from left to right, and from before backwards, rotating on its vertical axis, and bringing more of the left ventricle against the sides of the chest. The intraventricular pressure is now sufficient to cause the aortic and pulmonary valves to yield, and blood rushes into these vessels under the systole of the ventricles. The aorta and pulmonary artery fill with blood, elongate and curve; the heart, rotating so long as the ventricles are contracting, makes its impulse against the chest wall, and empties its contents into the arteries. The auriculo-ventricular groove now moves downward towards the apex of the heart, the ventricular walls relax and elongate, the pressure within them falls, and the blood from the over-full arteries is prevented from regurgitating into the ventricles by the semilunar valves coming into position. The closure of these valves creates the second sound of the heart. The ventricles are at this stage momentarily isolated, the auriculo-ventricular valves are closed, so also are the semilunar. This is the second time in the cardiac cycle that the ventricles have been shown to be cut off from the other part of the heart. We shall examine the question in greater detail presently. The great arteries now contract and shorten, the heart rotates backwards to the left, the auriculo-ventricular valves open, the auricles and ventricles, neither contracting nor dilating, assume a passive condition during a period known as the **pause**, the blood flows into the auricles, and from the auricles into the ventricles; the auricles now contract, and the whole process is repeated.

We have thus the contraction of the auricles, the contraction of the ventricles, and the pause. The time that each of these occupies has not been determined with accuracy; the results obtained by Chauveau and Marey in the horse show that the auricular systole is brief, the ventricular systole twice as long, and the pause equal in length to the ventricular systole; but the time values as given by them would cause the horse to have a pulse-rate of 60, which is abnormal. From 36 to 40 beats per minute is the normal rate, and this gives a period of 1·5 seconds for a complete cycle of the heart.

There is a well-marked interval between the contraction of the auricles and that of the ventricles, during which not only is the ventricle getting up pressure, but the papillary muscles are contracting to prevent the valves being pressed up further into the auricles. Chauveau draws especial attention in the horse to this interval, which has been named the **intersystolic period.** It must not, of course, be confused with the pause of the heart which follows ventricular systole. The auricles have a longer period of rest than the ventricles, but, as we shall see later, they are not entirely idle between each systole. One important point may here be conveniently stated, that no matter how fast the heart is beating, the frequency depends, not on the duration of the ventricular systole, but on the length of the subsequent pause.

Summary of Events occurring during a Cardiac Cycle.—Dividing the events into three periods, and starting with the contraction of the auricles, the following is a summary of the changes occurring in the heart:

First Period.—The contraction of the auricles completes the filling of the ventricles.

Second Period.—The auriculo-ventricular valves are closed, the ventricles contract, the aortic and pulmonary valves open, blood is pumped into the aorta and pulmonary artery, the impulse of the heart is made against the wall of the chest, the first sound is produced, the auricles fill with blood, and the whole is followed by a short pause.

Third Period.—The aortic and pulmonary valves close, the second sound of the heart is produced, followed by a long pause, during which diastole of both auricles and ventricles occurs, the auriculo-ventricular valves open, and blood flows into all the chambers.

The impulse of the heart, to which we have previously referred as being felt externally between the fifth and sixth ribs, is not given by the apex, but by the lower half of the left ventricle. There is no such thing as an apex-beat; the apex practically does not move as long as the heart is retained within the pericardium, but if the latter be opened, the apex is tilted forward with each contraction. The **Use of the Pericardium** is to prevent over-distension of the heart.

Cardiac Sounds.—There are four causes of sound in the heart, but as they work in pairs only two sounds are heard. We have previously indicated where these occur in the heart's cycle. The *first sound* is a long, booming one, and is made up of two causes—the muscle sound of the contracting ventricle and the closure of the auriculo-ventricular valves. The proof that the valves are not wholly responsible for the first sound is that the bloodless, beating heart still gives out a sound during ventricular systole.

The cause of the *second sound* has never been questioned; it is due to the closure of the aortic and pulmonary valves; it may be abolished by hooking these back, and re-established by releasing them. Under pathological conditions when the aortic valve is destroyed a murmur takes the place of the normal heart sound. When an animal is bled to death the second sound disappears before the first—in fact, it is abolished immediately the amount of blood propelled into the aorta is insufficient to distend this vessel properly.

As the first sound of the heart is heard from the beginning and during the major part of the systole of the ventricle, it is termed the 'systolic'; while the second sound, occurring at the beginning of diastole, is termed the 'diastolic.' On auscultation the two sounds are heard with unequal intensity at different parts of the cardiac area. They are heard better on the left side than on the right, not because the heart is nearer to that side than to the other, but for the reason that there is a larger gap in the left lung, which exposes the heart and allows its impulse to be felt against the chest wall. The two sounds are very accurately represented by the words *lūb dŭp*.

Intracardiac Pressure.—Most important additions to the physiology of the heart have been made by studying the pressure existing in its chambers. The pressure exerted upon the blood by the heart varies from moment to moment; the pump is for ever being charged and discharged, and both these processes depend upon the condition of internal pressure existing at the time. An examination of this internal pressure not only throws light upon the circulation, but also furnishes a better understanding of the mechanism of the heart itself.

It is interesting to note that the first experimental work done in this connection was by a French veterinary surgeon, Chauveau, in conjunction with a physicist, Marey. Their work, for beauty, originality, and exactitude, has only recently been exceeded. Observations were made on the horse by means of an instrument known as the *cardiac sound*, a diagram of which may be seen in Fig. 17. It is a double tube, having at its extremity two elastic balls separated so that when the apparatus is introduced into the heart, on the right side through the jugular vein, and on the left through the carotid artery, in each case one ball lies in the auricle and one in the ventricle. The air in the apparatus is compressed when the heart's cavities contract, and the compression moves a lever placed in connection with a recording surface. The introduction of the apparatus causes no pain, and as there are no sensory nerves in the lining membranes of the bloodvessels or heart, its presence gives rise to no inconvenience. Chauveau, in one of his memoirs, states that the pulse-rate was not disturbed, and the introduction of the instrument did not cause the animal to cease feeding.

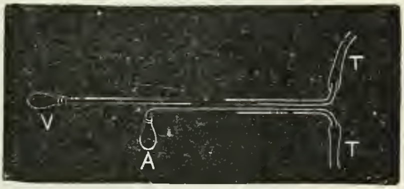

Fig. 17.—Diagram of Cardiac Sound.

A, Elastic ampulla for auricle; V, for ventricle; T, tubes connected with recording tambours.

A tracing taken by means of the apparatus just described is seen in Fig. 18. In it may be seen curves obtained simultaneously from the auricle and ventricle; the vertical dotted lines indicate coincident periods in both chambers. Taking the auricular curve, there is a sharp, sudden rise, indicating auricular systole, followed by a sudden fall in pressure, and the contents of the chamber are discharged. This is succeeded by two minor rises and falls in pressure before the pause in the heart's cycle D is reached. The curve of intraventricular pressure shows a slight and temporary rise at the moment the auricle reaches its maximum of pressure, and immediately afterwards a sharp, sudden rise in the intraventricular pressure starts. The pressure is maintained for a short time when once it has reached its maximum,

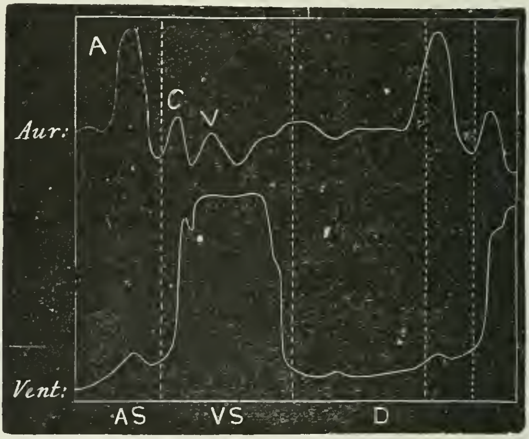

Fig. 18.—Curves of Endocardiac Pressure taken with Cardiac Sounds.

Aur., Auricular curve; *Vent.*, ventricular curve; AS, period of auricular systole, including relaxation; VS, of ventricular systole, including relaxation; D, pause.

and the curve is in consequence flattened; this flattening is called the *systolic plateau*, and is followed by an abrupt fall the moment the pressure within the ventricles is sufficiently low to allow the aortic and pulmonary valves to close. The fall in pressure which represents the end of the ventricular systole is followed by the pause D, and this is once more succeeded by a contraction of the auricles.

All that we have attempted to do in the above is to focus attention on the fact that certain positive and negative waves of pressure are constantly occurring in all chambers of the heart. Their shape on a recording surface depends upon the nature of the apparatus employed; their significance remains, and must now engage our attention.

There are three 'standard movements' in the heart to which other cardiac events may be referred in point of time; in the measurement and interpretation of pulse tracings in clinical work these are important landmarks. One is the *closure* of the semilunar valves of the aorta and pulmonary artery, another is the *opening* of the auriculo-ventricular valves. The first is known for brevity as the 'S.C. period,' the second is known as the 'A.O. period.'

In Fig. 18 the S.C. period occurs near the end of the ventricular plateau, just when the pressure in the ventricle becomes less than that in the aorta and pulmonary artery; the A.O. period occurs at the bottom of the down-stroke. Between these two points, brief as the period is, there exists within the heart rather a peculiar condition: the semilunar valves are closed, but the pressure in the ventricles is still too high to admit of the auriculo-ventricular valves opening, so that for this brief period no blood is entering the ventricles, which are screened off from all parts of the circulatory system. This period is known as the *postsphygmic.* Meanwhile the ventricular walls are relaxing, and as the cavity of the ventricle expands the pressure falls sufficiently to allow the auriculo-ventricular valves to open, and blood pours in from the auricle.

This is now the period of heart pause, during which both auricles and ventricles are filling simultaneously; it is succeeded by the contraction of the auricles, by which the ventricles are still further distended, and under the steadily increasing pressure in the ventricles the auriculo-ventricular valves are closed. This point occurs in Fig. 18 shortly after the beginning of the upstroke on the ventricular curve. The closure of the auriculo-ventricular valves is referred to as the *third standard movement.* The ventricles are now full of blood, shut off from the auricles by the auriculo-ventricular valves, and shut off from the general circulation by the closed aortic and pulmonary valves. This period, which is extremely brief, is known as the *presphygmic,* the period of rising pressure, or, as Stewart graphically puts it, the period during which the ventricles are 'getting up steam.' No blood can leave the ventricles until the pressure in their cavities rises above the aortic and pulmonary pressures. With the opening of the semilunar valves the blood is leaving the heart, and it continues to leave it during the period shown on the tracing as the systolic plateau.

If Fig. 18 be again referred to, and the curve given by the auricles examined, three well-marked waves will be seen; the first and largest, known as 'A,' we have previously referred to as corresponding to the contraction of the auricle; the second positive wave, known as 'C,' occurs during the rising pressure in the ventricles, and is probably due to the bulging of the auriculo-ventricular valves into the interior of the auricle. Chauveau, having experimented with a finger in the contracting auricle of the horse, says this upward bulging does occur. The cause of the third wave, known as 'V,' is not yet agreed upon. The interest of these auricular curves is mainly clinical; similar waves may be observed in veins near the heart, and the venous pulse thus observed may be employed to indicate irregularities in auricular contraction. We shall see presently that the contraction of the heart is initiated in the right auricle, so that a clinical examination of the behaviour of this cavity through the medium of the jugular pulse is a method of diagnosis of the utmost importance. In modern investigations of heart irregularities the most valuable information is being afforded by the A to C interval, or the time distance between the waves representing auricular and ventricular systole. In Fig. 19 may be seen a venous pulse-tracing from the dog in relation to auricular and ventricular contraction. The information thus obtained regarding the condition of the auricle may be compared with that obtained by the cardiograph and from the pulse-tracing in relation to the condition of the ventricle.

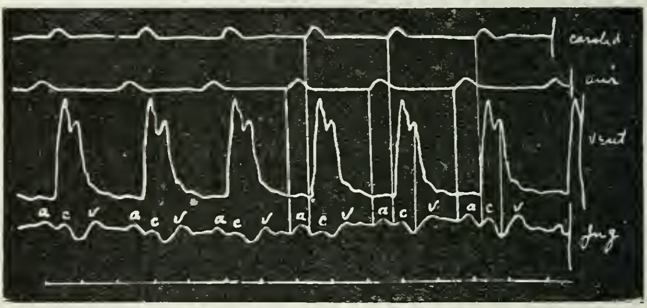

FIG. 19.—SIMULTANEOUS RECORD OF JUGULAR PULSE, VENTRICULAR CONTRACTION, AURICULAR CONTRACTION, AND CAROTID PULSE, IN THE DOG (CUSHNY AND GROSH).

a, *c*, *v*, The three elevations of the jugular pulse. (Time-trace, fifths of a second.)

Intracardiac Pressures.—The positive and negative pressures in the heart in large dogs have been measured with the following results:

Right auricle: maximum positive, 20 mm. ($\frac{3}{4}$ inch) of mercury; minimum negative, −10 mm. ($\frac{1}{2}$ inch).
Left ventricle: maximum positive, 230 to 240 mm. ($9\frac{1}{4}$ to $9\frac{1}{2}$ inches); minimum negative, −30 to 50 mm. ($1\frac{1}{4}$ to 2 inches).
Right ventricle: maximum positive, 70 mm. ($2\frac{3}{4}$ inches); minimum negative, −25 mm. (1 inch).

In the horse the maximum pressure in the left ventricle has been found to be from 178 to 318 mm. of mercury (7¼ to 12¾ inches), or a column of blood 2·4 to 4·3 metres (9 to 14 feet) in height. In the right ventricle of the same animal the maximum pressure was 34 mm. (1½ inches), equal to a column of blood 0·46 metre (1½ feet) high.

Starling* points out that, provided the blood-pressure in the heart does not exceed the above physiological limits, and the inflow of blood remains constant, it is immaterial to the heart what blood-pressure it has to contend with. The more the blood-pressure rises, the greater the quantity of blood which passes through the coronary arteries, and consequently the better blood-supply to the heart muscle.

The negative pressure within the heart has not been satisfactorily explained. According to one view, the heart behaves like the bulb of a flexible syringe, which is discharged by pressure and filled by the elastic dilatation of its own walls; but there are objections to this view, inasmuch as no elastic dilatation can be demonstrated by experiment, nor have any of the other views put forward been supported by conclusive experimental evidence. The explanation that the dilatation was due to the aspiratory effect of the air-tight thorax may be negatived by the fact that the negative pressure may be still recorded with the thorax open. In fact, the explanation of cardiac dilatation has yet to be found.

The **Cardiac Impulse** has been studied by means of an instrument termed a *cardiograph*, which transmits the impulse of the heart on the chest wall to a recording apparatus. Curves so obtained are often difficult to interpret; they are the graphic record, not of one event, but of a series of events, the chief of which are variations in ventricular pressure and changes in volume. In Fig. 20 is a cardiogram which shows a small elevation corresponding to auricular contraction, followed by a large rise due to ventricular systole, with a sudden and then prolonged drop indicating relaxation of the ventricles. In the horse the impulse of the heart occurs on the cartilages of the fifth and sixth ribs, close to the articulation with the rib, the centre of the shock being the fifth intercostal space (see Fig. 45, p. 107).

The Capacity of the Heart may be ascertained by enclosing it in a chamber termed a *cardiometer*, and measuring the change of volume during systole and diastole.

Observations so conducted show that the ventricle does not empty itself at each systole; as much as one-third of the blood may be left in it. Colin, many years ago, showed this for the horse, and stated that not more than two-thirds or three-fourths of the ventricular charge was expelled. The quantity of blood with which the heart is capable of dealing cannot be ascertained by measuring the capacity of the chambers. Munk gives the capacity of the horse's ventricle at 1 litre (1·76 pints), equivalent, roughly, to 1 kilogramme (2·25 pounds) blood, and states that each ventricle contains one-thirtieth of the blood in the body, so that when both contract one-fifteenth of the total blood is ejected. Both ventricles deliver the same amount of blood, for there is as much entering the heart from the pulmonary veins as from the venæ cavæ.

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* 'The Law of the Heart,' E. H. Starling, M.D., F.R.S., 1918.

Work of the Heart.—This may be calculated if we know the amount of blood being discharged from the heart at each stroke, and the pressure against which it is propelled. The amount pumped out at each systole of the ventricle is liable to great variation; at least, such are the results of experiments on the dog, in which animal it has been shown that the contraction volume of the left ventricle diminishes as the size of the animal increases. It is obvious that the right ventricle does less work than the left, for the reason that it has to pump the same volume of blood against a much smaller *peripheral resistance;* it has been said, indeed, that the right heart does one-quarter the work of the left.

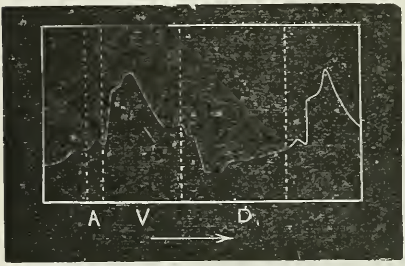

FIG. 20.—CARDIOGRAM TAKEN WITH MAREY'S CARDIOGRAPH (STEWART).

A, Auricular systole; V, ventricular systole; D, diastole. The arrow shows the direction in which the tracing is to be read.

If we take the amount of blood pumped at each stroke into the aorta of the horse as about 1 kilogramme (2·25 pounds) in weight, and the pressure under which it is forced upwards as equivalent to a column of blood 3·048 metres (10 feet) in height, then the work of the left ventricle at each stroke is equal to 10 kilogrammes (22·5 pounds) raised 0·304 metre (1 foot) high, or for twenty-four hours, allowing the work of the right heart to be one-fourth that of the left, 212,275·86 kilogramme-metres (1,539,000 foot pounds). This amounts to about one-thirtieth of a horse-power per diem; Munk places it at one-thirty-sixth of a horse-power. If the amount of blood expelled by the left ventricle at each stroke be equal to 1 kilogramme, then in a state of repose the entire blood in the body of a horse passes through the heart in about thirty beats, or in forty-five seconds. Munk says that in the horse the entire blood passes through the heart in fifty seconds, in the ox in forty seconds, and in the dog in twenty seconds. Since the amount of work performed by the heart is increased during exercise, the above calculations only hold for a horse in a state of repose. During work a larger quantity of blood passes through the heart and a high blood-pressure occurs under the influence of the muscular walls. This high pressure is necessary in order to force open the aortic valves and insure that there shall be a sufficient flow of blood through the parts supplied even by the finest vessels. Starling* points out that the heart muscle does its work with the greatest judgment and adjusts its energy to the mechanical conditions present. If the muscle receives a larger quantity of blood, the heart temporarily dilates and the muscle fibres lengthen; this lengthening increases the energy of the heart muscle, and with a large quantity of blood passing into the coronary arteries the muscle substance is kept well supplied with oxygen, the tone of the heart is restored, and the organ returns to its normal size, although doing more work. A diseased or fatigued heart does not recover, but may remain dilated during the whole work period, and eventually under stress become permanently enlarged.

Coronary Circulation.—The vascular system which supplies the heart substance is lodged in grooves in its wall, and much discussion has arisen, not only as to the moment at which the arteries receive their supply, but also as to the effect on the coronary bloodvessels of the contraction of the surrounding heart muscle. It is now generally admitted that the coronary arteries receive their blood during the ventricular systole, and not, as was originally thought, during the closure of the aortic valves. The latter, as we have seen, do not cover the openings of the coronary arteries. The question of the effect of the heart's contraction on the vessels lodged in its walls is far more difficult of solution. If the squeezing of the heart will assist the passage of blood in one direction it must retard it in another, for the veins and arteries lie side by side, the blood flowing in opposite directions; the effect on the thick-walled arteries is, however, less than on the thin-walled veins. When the ventricle begins to contract, it can be shown that the pressure and velocity in the coronary arteries is increased; but as the contraction proceeds, and the muscle is, as it were, being wrung, the coronary vessels are clamped, and the blood in the arteries is driven back on the aorta, while that in the veins is forced onwards to the right auricle. At diastole the coronary arteries at once refill, and, as we have seen above, a further charge is pumped in at the beginning of contraction. Other experiments appear to show that with each systole of the heart the coronary system is emptied towards the venous side, and at each diastole it is filled.

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* 'The Law of the Heart,' E. H. Starling, M.D., F.R.S., 1918.

The effect of occluding the coronary arteries is of the utmost practical interest. If all the arteries be clamped the heart at once stops; but if the observation be limited to one vessel only, that portion of the ventricle supplied by it ceases to beat. The arrest of the ventricle is a curious condition, giving rise either at once or soon after to the phenomenon known as **fibrillar contraction,** in which the surface of the heart presents vibrating, twitching, disorderly movements, to which the term *delirium cordis* has aptly been applied. It is as if each fibre of the heart were irregularly contracting on its own account, independently of its neighbours.

Fibrillation of the auricles may also be experimentally produced, but the auricles, unlike the ventricles, appear to possess a capacity for returning to co-ordinate contraction. Considerable attention is now being paid clinically to fibrillation of the auricles, which Lewis* finds is the commonest persistent irregularity exhibited by the human heart, constituting approximately 50 per cent. of all such cases. He has also observed it in the horse, and it is quite likely that it may turn out to be a relatively frequent condition. Though fibrillation of the ventricles means immediate death, fibrillation of the auricles does not.

The Cause of the Heart-Beat.—It seems incredible that the use of the heart should have remained unknown until the early part of the seventeenth century. Even now some of the chief features in its working are obscure, and concerning one of them, the cause of the heart-beat, much difference of opinion exists.

An ordinary skeletal muscle is under the control of the nervous system by which its movements are carried out, but the hollow heart muscle, whose never-ceasing action is maintained for years with perfect regularity, is known to beat independently of any nervous supply. The evidence of this is conclusive; the hearts both of the frog and of mammalia are capable under similar conditions of contracting rhythmically for hours, even for days, when entirely removed from the body, and therefore when no longer in connection with the nervous system. The discovery of nervous bodies called ' ganglia ' in the substance of the heart wall at once appeared to afford a solution of the vexed problem of why the heart was capable of spontaneous movements, but it was shown that the embryonic heart was capable of spontaneous movement before any sign of ganglia appeared in its walls. The position in which the inquiry stands to-day is practically represented by the above; physiologists are not agreed as to whether the heart muscle, independently of its ganglia, sets up its own movements, or whether these are initiated by the nervous elements embedded in its walls. The former is called the *myogenic,* the latter the *neurogenic,* theory. Both these views must be briefly examined.

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* T. Lewis, M.D., D.Sc., ' Auricular Fibrillation,' *Heart*, vol. i., No. 4, 1910.

The Neurogenic Theory.—In the walls of the frog's heart, and those of a few other cold-blooded animals, intrinsic nerve ganglia have been discovered, and from this it has been argued that some such arrangement exists in the hearts of mammalia. This, however, has never been demonstrated beyond doubt. Three intrinsic ganglia, known after their discoverers as Remak's, Bidder's, and von Bezold's, are situated mainly in the venous end of the heart—viz., in the auricles, at the junction of auricle and ventricle, and in the interauricular septum. Ganglia have been described as occurring in the ventricles, but at present no conclusive evidence has been brought forward to prove this.

The neurogenic theory requires that in these ganglia, situated, it will be observed, at that end of the heart which initiates the contraction, impulses are originated which pass out to the neighbouring muscular tissue, and give rise to a regular sequence of events. But there is no evidence in vertebrates that the heart possesses an intrinsic motor nervous system charged with the spontaneous production of rhythmical contractions. The whole of the nerves in a strip of heart wall may be cut without the tissue losing its property of spontaneous contraction.

The *Myogenic Theory* demands that the heart muscle, independently of any nervous supply, shall possess the power of contracting automatically and rhythmically, and the experiment last named lends considerable support to this theory. The contraction of the heart from base to apex is provided for by the A.V. bundle of conducting muscular tissue described at p. 33, which links up auricle and ventricle, while the base of the heart is provided with muscle, more pronouncedly automatic than that found in the ventricles, which insures the normal sequence of events from base to apex.

Within the right auricle, below and to the right of the coronary sinus, lies the auriculo-ventricular node (Fig. 12), the commencing portion of the A.V. bundle; if this connection be cut or compressed, disturbance of conduction follows known as **heart-block.**

In a work of this kind it is not necessary to enter deeply into vexed questions such as the one we are here considering, but two more points in favour of the muscular theory of contraction may be briefly mentioned.

The normal direction of the wave of contraction of the heart muscle from auricle to ventricle may, under certain conditions, be reversed—viz., from ventricle to auricle. For example, if a ligature be passed around the heart of the frog between the sinus and the auricle (Stannius's experiment), the auricle and ventricle cease to beat; if now the ventricle be stimulated to contract, the auricle follows. On the theory of muscle conduction this experiment can be explained, but not on that of nerve conduction.

The balance of evidence is in favour of Gaskell's myogenic theory as the conducting medium of automatic action, but this still leaves the question of the nature of heart automaticity untouched.

Heart Automaticity.—A heart, even one which has been apparently dead for some time, may be revived by placing it in an atmosphere of oxygen and transfusing through its vessels a solution containing sodium chloride, calcium chloride, potassium chloride, sodium bicarbonate, and grape-sugar. It was Ringer who was the first to show that a fluid of a definite strength containing sodium, potassium, and calcium chlorides would keep the frog's heart beating for days; but it is only recently that the mammalian heart, and one even that has been apparently dead some days, has been shown to be capable of resuscitation. Not only are sodium, potassium, and calcium chlorides required to be of a definite strength, but practically no substitute is efficient. The dextrose and sodium bicarbonate are added to increase the efficacy of the work, but they are not essential; on a diet of inorganic salts the heart is capable of beating rhythmically for days.

We have at p. 8 referred to the action of a 0·9 per cent. solution of sodium chloride as a physiological solution. It is sodium chloride which, in a strength of 0·5 to 0·6 per cent., is mainly responsible for the normal osmotic pressure of the blood, and though alone it is not capable of maintaining the heart-beat, nor of furnishing the tissues with all the inorganic material they require, nevertheless it is more effective in these respects than any other single salt. The presence of calcium, though the amount in blood is only small, appears to be necessary to contraction; at any rate, the addition of calcium to the 'fed' heart, or its application to the isolated strip, not only brings on contractions, but increases the length of time during which they are continued. The physiological effect of potassium appears to be connected with relaxation rather than with contraction.

Facts such as the above suggest that the heart is capable of generating in its own substance a stimulus to contraction, and the hypothesis of an *inner stimulus*, though it takes us no nearer to a conception of the nature of the stimulus, assists the imagination. It is not considered that the inner stimulus is represented by the inorganic salts, but rather that in the presence of these it is capable of doing its work.

The Physiological Properties of Cardiac Muscle differ from those of skeletal muscle. The stimulation of skeletal muscle with a weak current causes a weak contraction, with a strong current a more powerful contraction. But the heart muscle behaves differently; the amount of contraction it exhibits under stimulation is the full amount which it is at the time capable of exhibiting, no matter whether the current be a weak or a strong one, the ' all or none ' effect. This remarkable difference has been explained by the fact that in skeletal muscle the fibres are isolated from one another, while in heart muscle they form a continuous sheet, and the excitation travels from fibre to fibre.

Another difference distinguishing heart from skeletal muscle is the reaction to repeated electrical stimulation. If a series of rapid induction shocks be passed into skeletal muscle, it is thrown into a condition known as *tetanus ;* but heart muscle cannot be tetanised, for the reason that electrical stimuli applied to it during the period of its contraction produce no effect whatever. It is only during diastole that a response to stimulation is obtained.

The non-irritable period of the heart muscle during its systole is named the **refractory period,** and the response to stimulation obtained during diastole is described as an **extra contraction.** Having executed this contraction out of its regular sequence, the heart makes the succeeding pause longer than usual, by which means it picks up its rhythm as though it had never been disturbed. The pause is known as a **compensating pause.**

The heart muscle stands alone in being non-irritable during its period of actual contraction; neither skeletal nor plain muscle exhibits this phenomenon. The refractory period is in all probability connected with the internal metabolic processes concerned in the building up of the heart's contractile material, and it appears at present impossible to separate these from the fundamental processes of rhythmicity.

The direction of a contraction through the mammalian heart is from auricles to ventricles via the auriculo-ventricular bundle; the rate of conduction through this bundle is slower than that through the ordinary heart muscle, which explains the slight pause between the contraction of the auricles and that of the ventricles. The rhythm set by the auricles is under normal conditions taken up by the ventricles; but experimentally it can be shown that interference with the A.V. bundle may lead to the rhythm of the ventricles being slower and independent of that of the auricles. The precise results obtained depend upon whether there is a partial or complete block between the auricles and ventricles. The condition thus experimentally produced has its clinical counterpart in irregularities due to heart-block.

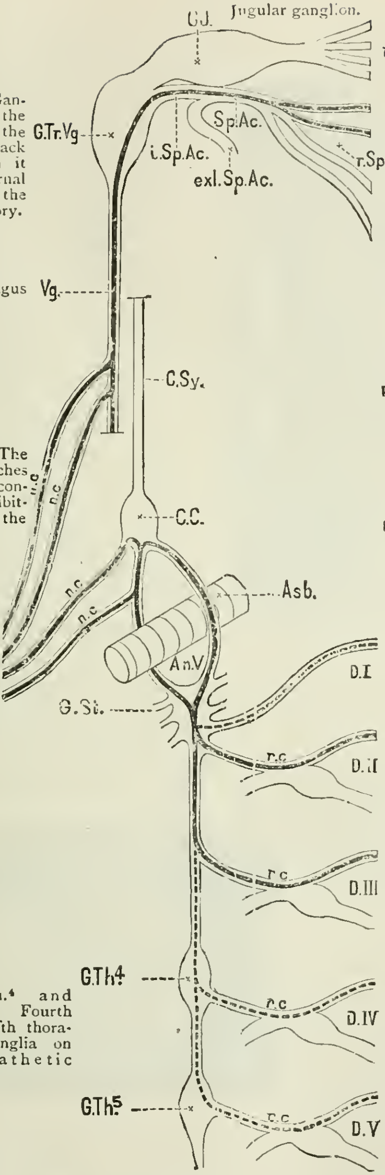
One word more may be said in connection with the transmission of a contraction through the heart. Chauveau has shown that the two auricles in the horse do not contract precisely together; there is a slight delay in the contraction of the left, and this is explained by saying that the transmission of the contraction from right auricle to left auricle takes time.

Nervous Mechanism of the Heart.—Up to this point the question of the rhythmical contraction of the heart has been considered; we have now to take up another and distinct question—viz., the influence of the nervous system in regulating the activity of the heart. The heart receives nerve supplies from two portions of the central nervous system: one is concerned with the transmission of impulses which slow or stop the heart, hence called *inhibitory ;* the other conveys to the heart impulses which stimulate or augment the activity, and are in consequence known as *augmentor* or *accelerator* nerves. From the **vagus** are derived the inhibitory effects, and from the **sympathetic** the augmentor. It is obvious that these nerves are antagonistic, the one endeavouring to slow the heart, the other pressing it on. The balance between these two opposite conditions results in the normal rate of heart-beat.

Not only have these two nerves opposite functions, but they are also structurally different, the vagus being a medullated, the sympathetic a non-medullated nerve.

An immense amount of work has been done in endeavouring to elucidate the physiological effects on the heart of the vagus and sympathetic, and the results have not always been concordant. This may be due to the fact that the frog has usually furnished the experimental material. The physiology of this creature's heart is known more completely than that of any other animal's, but what is known cannot always be held true of the mammal, owing to anatomical differences in the arrangements of the nerves.

In the frog there is a vago-sympathetic nerve in the neck, in which the fibres of both nerves are anatomically mixed, though functionally distinct; the mixing up does not occur in the chest, as in the mammal, but close under the skull. When this vago-sympathetic is stimulated, either inhibitory or augmentor effects may be obtained, according to which one of the set of nerve-fibres in the mixed nerve happens to be more efficiently stimulated. The mixing of the fibres takes place in the ganglion of the vagus nerve, which lies just outside the skull. If the intracranial fibres of the vagus are stimulated, the effect on the heart is



Jugular ganglion.

Right vagus.

G.Tr.Vg. Ganglion on the trunk of the vagus; the black line through it is the internal branch of the spinal accessory.

Inhibitory fibres from spinal accessory entering the vagus.

Vg. The vagus nerve.

C.Sy. The cervical sympathetic nerve.

nc., nc. The cardiac branches of the vagus conveying inhibitory fibres to the heart.

G.C. Inferior cervical ganglion.

Asb. Subclavian artery.

An V. Annulus of Vieussens.

nc., nc. Cardiac branches of the sympathetic conveying augmentor fibres to the heart.

G.St. Ganglion stellatum.

D.II, D.III. The inferior roots of the second and third spinal nerves, passing by means of r.c. the ramus communicans to the ganglion stellatum. These are the augmentor fibres, passing both by the annulus and inferior cervical ganglion to the heart by nc. nc.

G Th.^{4} and G.Th.^{5} Fourth and fifth thoracic ganglia on sympathetic chain.

The dotted line in certain thoracic nerves, D.I., D.IV., and D.V., indicates that they may contribute augmentor fibres to the sympathetic.

Fig. 21.—Diagrammatic Representation of the Cardiac Inhibitory and Augmentor Fibres in the Dog (Foster).

The upper portion of the figure shows the inhibitory, the lower the augmentor fibres.

purely inhibitory, and if the fibres of the sympathetic are stimulated just before they enter the ganglion, the effect is entirely augmentor. In the mammal the vagus and sympathetic are distinct, even if, as in some animals, they run in the same sheath, while accelerator fibres do not join the sympathetic until it enters the thorax.

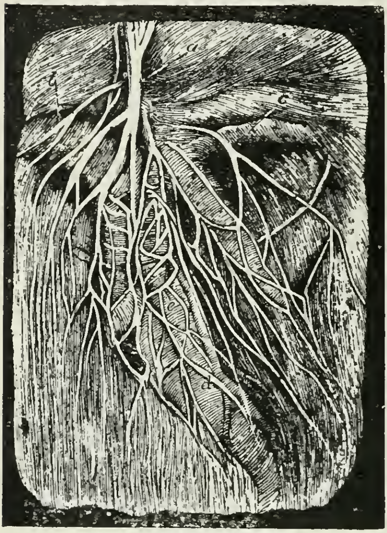


Fig. 22.—Nerves on the Surface of the Horse's Heart (Pettigrew).

a, Nerve descending to the auricle; *b*, *c*, coronary vessels; *e*, *d*, vessels in anterior ventricular furrow.

In the mammal the vagus arises from the medulla; the inhibitory fibres it receives are derived from the spinal accessory and join the vagus within the skull; the cardiac branches of this nerve are given off from it in the thorax. The sympathetic supply to the heart comes out of the spinal cord certainly at the second and third dorsal nerves, probably at others, and by means of the *rami communicantes* passes to the stellate ganglion, thence to the inferior cervical ganglion on the cervical sympathetic trunk, and from this ganglion to the heart The above arrangement applies especially to the dog, and is shown diagrammatically in Fig. 21; it is not quite the same for all mammals. The rich plexus of nerves on the surface of the horse's heart may be seen in Fig. 22, and that of the calf in Fig. 23.

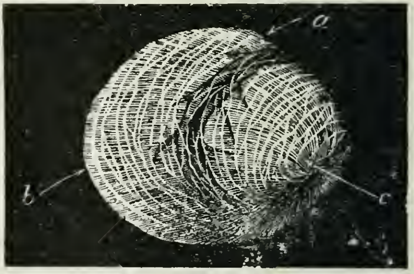


Fig. 23.—Nerves on the Surface of the Left Ventricle of the Calf (Pettigrew).

The nerves take a spiral direction, like the muscle fibres; *c*, apex of ventricle.

Function of the Vagus.—If the vagus in the neck be cut and its peripheral end stimulated, the rate of the heart-beat is slowed and the force of the beat diminished. If stronger stimulation be applied, the heart stops in a condition of dilatation, and becomes swollen with blood.

Slowing of the heart-rate is the most prominent effect of vagus stimulation, and this in the mammal is more apparent in its effect on the auricles than on the ventricles. The strength of the ventricular contraction may continue undiminished at the time the auricles are suffering from inhibition, and should the stimulation be sufficiently strong to cause the auricles to cease contracting, the ventricles for a brief time are inhibited, and then beat again independently. In other words, in the mammal the vagus is essentially an auricular nerve. The phenomenon of inhibition does not show itself immediately on the application of the stimulus; there is at least one contraction before the heart slows or ceases to beat. This delay is known as the **latent period** (Fig. 24). In some animals, such as the cat, even the stronger stimulation of the vagus only slows the heart; it does not stop it; whereas in the dog relatively weak stimulation may bring the heart to a standstill. Fig. 25 shows the effect on blood-pressure of weak and stronger stimulation of the vagus.

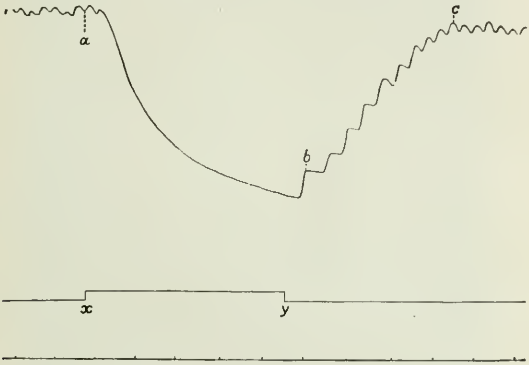


FIG. 24.—TRACING SHOWING INFLUENCE OF THE ARREST OF THE HEART ON BLOOD-PRESSURE, DUE TO STIMULATING THE VAGUS (FOSTER).

x, Marks on the signal line when the current is thrown into, and *y* shut off from the vagus. The time-marker below marks seconds. *a* corresponds in point of time with *x*; the heart does not at once cease to beat. The first beat, *b*, occurs a short time after shutting off the current. The notches in the tracing are due to the beats of the heart.

Inhibition does not last long; it may, of course, cause death, but as a rule it is overcome and the heart starts again. Moderate stimulation of the vagus sufficient to slow the rate may be tolerated for some time. In the frog the same escape from inhibition may be seen. The heart subsequently makes up for lost time by working at a greater rate or strengthening its contractions, until it regains its usual rate of working. When an inhibited heart behaves in this way, its action is spoken of as *secondary augmentation*, and the phenomena, though best seen in the frog, may also, though in a less marked degree, be seen in the mammal.

Reflex inhibition of the heart may arise through a sensory surface, as in painful impressions, or in a blow on the abdomen, and in other ways. Afferent impulses—that is, impulses conveyed *to* a nerve centre from without—must pass through the centre from which the inhibitory fibres of the heart arise, and though such a centre has not been defined with exactitude, the existence of a *cardio-inhibitory centre* in the medulla is undoubted. From this centre impulses issue which in a normal state throughout the whole life of the animal are passing down the vagus, keeping a constant watch and control over the rate of the heart, and the proof that such a view is not a fanciful one is shown by the result of cutting off these impulses by dividing both vagi, when the frequency of the heart-beats is greatly increased. This constant action of a nerve centre is known as *tonic activity*, and this in all probability is the outcome of impulses flowing into it through sensory nerves; a mechanism so arranged produces what is known as a *reflex tonus*.

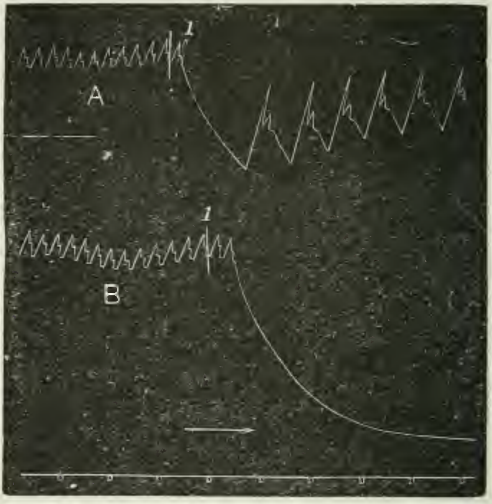


FIG. 25.—BLOOD-PRESSURE TRACINGS: RABBIT (STEWART).
Vagus stimulated at 1; stimulation stronger in B than in A (Hürthle's manometer).

The *Action of Poisons on the Heart* has been appealed to in order not only to decide their pharmacological effect, but also as a physiological means of research in connection with its nervous mechanism. *Atropine* causes the heart-rate to become quickened, on account of the inhibitory effect of the vagus being suspended. If the vagus under these conditions be stimulated, no inhibition follows, and it is argued that this is due to a paralysis of the nerve terminations of the inhibitory fibres in the heart muscle, much the same as that of the motor end-plates in muscles under the action of curare. *Muscarine*, a poison obtained from certain mushrooms, causes the heart to slow down, and finally to stop. *Pilocarpine* has much the same effect, and it is assumed that both these alkaloids stimulate the inhibitory fibres. This view is strengthened by the fact that atropine abolishes the inhibitory effect produced by muscarine and pilocarpine, and it is considered that this result is due to the paralysis of the terminals of the inhibitory fibres in the heart muscle.

Function of the Sympathetic Nerve.—The course of the accelerator fibres derived from the sympathetic has been previously described. Their distribution in the heart is mainly to the ventricles. The vagus fibres, it will be remembered, are principally distributed to the auricles. If the sympathetic trunk in the neck of the mammal be stimulated, no effect follows, for, as Fig. 21 shows, there are no accelerator fibres above the inferior cervical ganglion. If certain branches issuing from this ganglion be stimulated, the heart-beats are increased in frequency, and sometimes, but not always, in force; in other cases they are increased in force and not in frequency. There is reason to think these differences are explained by the probability that the accelerator fibres consist of two sets, one increasing the frequency of the heart-beat and the other increasing the force. On stimulation, accelerator effects can be obtained from either the right or left ganglion, but the augmentor effect is best obtained from the left side.

The accelerator fibres, like the inhibitory, are in a state of constant or tonic activity, as evidenced by the fact that, if they be divided, the heart-rate is thereby decreased. It has been assumed that this constant activity is carried on by a centre situated in the medulla, and that to it pass afferent impulses of a reflex nature which either increase or decrease its activity. No better example of a reflex stimulation of the accelerator centre could be witnessed than the fright of a nervous horse startled; the heart may almost be heard thumping against the chest wall.

No such accelerator centre has actually been located in the medulla, but the probability of its existence is considerable. On the other hand, it is not a physiological necessity; acceleration might be brought about by inhibition of the cardio-inhibitory centre, and experiment has shown the possibility of the effect being produced through this channel.

The Nature of Inhibition.—The discovery of the inhibitory action of the vagus was a great addition to physiological knowledge; it settled the important point that such an effect could be produced through the nervous system, and has been the means of adding considerably to our physiological knowledge of other organs besides the heart. The actual means by which inhibition in the heart is brought about is still a matter of speculation; the view most generally accepted is that propounded by Gaskell. He regards the vagus as the protecting nerve of the heart, and reasoning from the observed fact that after its stimulation and consequent inhibition there is on recovery an improvement in the rate or force of the heart-beats, he concludes that during inhibition there is a building up—*anabolism*—of the muscular tissue which results in the improved condition of the heart. Such changes are of an opposite character to those occurring during contraction, which are of a *katabolic* or tissue-destroying nature, by which complex substances are converted into simpler ones, with the production of heat and energy. The latter changes are regarded as brought about by the sympathetic system. During inhibition the heart is being repaired, during contraction its substance is being used up, and Gaskell believes that all muscular tissue is similarly provided with anabolic and katabolic nerves.

The Depressor Nerve.—The nervous mechanisms considered up to this point are concerned in bringing about some modified action of the heart, under the guiding influence of a nerve centre in the medulla. We have now to consider the case where a nerve running *from the heart* to the medulla is engaged in a regulative action which, unlike that of the vagus or sympathetic, is not a direct action on the heart itself, but is brought to bear indirectly on the heart mainly through the instrumentality of the vascular (arterial) system. This nerve is the *depressor*. It is a branch of the vagus distributed to the heart—some say to the walls of the aorta—and from there runs up the neck as a separate branch in the horse, cat, and rabbit, but in other animals is contained in the trunk of the vagus. It joins the superior laryngeal nerve, and finally reaches a centre in the medulla which regulates the movements of the bloodvessels of the body, known as the *vasomotor centre*. The impulses which pass along it are afferent—viz., they pass to the central nervous system and not out of it. The heart in this way is placed directly in communication with the centre which presides over the vascular system, a centre by whose varying activities the arteries of the body are made smaller (constricted) or larger (dilated), according to the needs of the system. If the heart is labouring and its muscular structure becoming weakened, impulses pass up the depressor to the vasomotor centre, resulting in impulses being sent out which cause the abdominal arteries to dilate and hold more blood. By this means the peripheral resistance is diminished, the blood-pressure falls, and the heart is eased, since it now has less work to do in ejecting its contents.

If the depressor nerve be divided, no effect follows; if the end in contact with the heart be stimulated, there is no result; but if the central or upper end be stimulated, the blood-pressure falls (see Fig. 26).

By some the depressor nerve has been described as the sensory nerve of the heart, as they hold that there are signs of pain when it is stimulated in an animal not under an anæsthetic. But this view is not generally accepted, and as a matter of fact the heart may be handled, pinched, pricked, or otherwise injured, without provoking the least sign of pain on the part of the animal. Colin's experiments in this direction on horses appear quite conclusive. Not only is it considered that the external surface is insensible to pain, but the internal surface also; for, as previously noted, the experimental introduction of foreign bodies into the cavities of the heart appears to produce no pain. Under pathological conditions the results are otherwise; foreign bodies, so common in the heart of the cow, cause great suffering, therefore there must be sensory nerves, though normally their excitability is probably low.

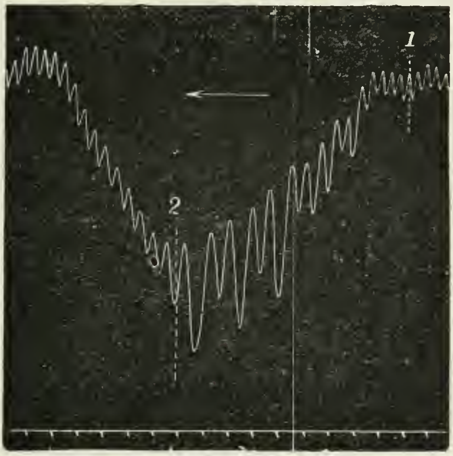


FIG. 26.—BLOOD-PRESSURE TRACING: RABBIT (MERCURY MANOMETER) (STEWART).

Central end of depressor stimulated at 1; stimulation stopped at 2. Time-trace, seconds.

It is supposed that in the distending aorta the sensory nerve endings are stimulated, and that the impulses so obtained are conveyed to the medulla by the depressor, and increase the tonic activity of the cardio-inhibitory centre. It can certainly be shown experimentally that every contraction of the heart sends a series of impulses up this nerve, which give rise not only to a reflex dilatation of the splanchnic arterioles, but also to a reflex cardiac inhibition.

We have now seen how complex are the influences exercised by the nervous system on the rhythm, force, and tone of the heart muscle, the moderating influence in these directions exercised by the vagus, and the stimulating functions of the sympathetic. The factors determining which influence at the moment is best suited to the existing conditions are to be found in the periphery, and not in the central nervous system; from the periphery—viz., skin, muscles, viscera, bloodvessels, and heart—impulses are transmitted to the brain which are obeyed by the cardio-inhibitory or accelerator centres in the medulla.

The Chemical Stimulus.—One further feature still remains for consideration, and that is the influence of certain 'internal secretions' on increasing or diminishing the function of the heart muscle. It is now known that the adrenal capsules and pituitary body are capable of furnishing extracts which, when introduced into the circulation, exercise a powerful effect on the heart. An extract of the medulla of the adrenal capsules increases the rhythm, force, and tone of cardiac muscle. An extract of pituitary body contains two substances; one increases the tone, but does not affect the rate of rhythm of the muscle, while the second diminishes the force of the heart-beat. It may well be that these ductless glands pour into the circulation their various secretions in the proportions suited to the most efficient working of the heart, and by their action on the nerve-centres maintain them in effective working order.* The action of these internal secretions on the movements of the bloodvessels will be referred to later.

Electrical Changes in Heart Muscle (see Chapter XIII.).

Pathological.

Disease of the heart in the lower animals is uncommon. It might have been thought that horses would be particularly exposed to this class of trouble, bearing in mind the enormous strain placed on the heart during labour, and the utter want of consideration shown by the vast majority of those who ride and drive them. But it is not so. The hearts of horses exposed to the greatest strain seldom show any pathological change; probably the most uncommon lesions found on post-mortem examination are those affecting the heart. The heart may dilate under strain, but such dilatation when accompanied by hypertrophy is compensated, and no indication of trouble exists during life. It is evidence of the gross strain to which horses are exposed that **ruptures of the heart** are by no means uncommon. It is strange they are not more frequent. They probably would be but for the saving reason that degenerations of the heart substance are rare. When the heart ruptures, it gives way in the auricle, where the wall is thinnest—so thin, indeed, that in certain parts of the auricle daylight may easily be seen through the tissue. It is generally the right and not the left auricle which suffers, showing how great is the resistance offered by the pulmonary vessels as the result of engorgement due to severe work.

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* See 'The Factors which make for an Efficient Circulation,' by Professor Sir E. A. Sharpey Schäfer, F.R.S., *British Medical Journal*, October 29, 1910.

Valvular disease is not unknown, but so rare that probably there is no practitioner with a large experience in the examination of horses for soundness who ever thinks of examining the heart! On the other hand, **irregularities** in the heart's action are very common; frequently purely functional in character, unassociated with organic change, they do not interfere with the usefulness of the animal. A horse condemned for heart disease on the strength of an intermittent pulse may remain a living reproach to the practitioner.

The views on heart disease in man have within the last few years been undergoing profound modification through the work of Mackenzie,* Lewis,† and other observers. It is too much to expect that the complete revolution in doctrine which these new ideas necessitate will be at once brought about; the process must be gradual, but when accomplished it will be found that very little modification from the views now put forward will be necessary. Briefly, the modern theory of the causes of **heart failure** looks to the heart muscle itself as the prime seat of disorder; indeed, the coarser and more obvious conditions, such as murmurs and irregularities, may not even be pathological, or, if pathological, are of secondary interest to the all-important inefficiency existing in the heart muscle. Mackenzie has presented a statement of the modern views of heart trouble in man, of which the following is a brief epitome:

The popular conception of heart failure is associated with valvular trouble, the thickened and shrunken valve producing incompetence, with leakage from the ventricle, distension of the auricle, stasis in the lungs, back pressure into the veins, with consequent dropsy. Functional murmurs may exist in a perfectly healthy heart under physiological dilatation; a tricuspid regurgitation may be regarded as a safety-valve function, as it is in certain diving animals; and a mitral regurgitation may exist for fifty years without crippling the heart in its work. Irregularities of the heart may not only be normal, but may even, within certain limits, be considered as evidence of the integrity of the heart muscle.

These unorthodox views from one who has confined his attention to the study of heart trouble for many years must cause even the most sceptical to pause. According to Mackenzie, the essential causes of heart trouble in man are consequent on **auricular fibrillation,** a condition which alters the whole aspect of the mechanism of heart failure. To the phenomenon of fibrillation attention has been drawn at p. 50. The muscle fibres, instead of contracting in a normal and orderly manner, contract irregularly, rapidly, and independently, so that the chambers not only cease to contract as a whole, but actually stand still, while all their fibres are in incessant movement. When this condition occurs in the ventricles, sudden death ensues; when it occurs in the auricles, death does not follow, for fibrillation cannot pass along the bundle connecting the auricles with the ventricles. The degree of heart failure which follows auricular fibrillation depends upon the extent to which changes have occurred in the structure of the heart muscle of both auricle and ventricle.

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* 'Heart Failure,' James Mackenzie, M.D., LL.D., *British Medical Journal*, April 8, 1911, p. 793.

† 'Clinical Disorders of the Heart Beat,' T. Lewis, M.D., D.Sc., F.R.S.

In severe inflammatory chest invasions of the horse, the heart, but especially its sac, may become acutely affected. There are few attacks of severe pleurisy in the horse which are not associated with **pericarditis,** followed not only by great thickening of the heart sac, but by more or less extensive effusion into it. The heart then becomes enveloped in a water jacket, and this greatly adds to the gravity of the case. In the above acute cases the heart muscle suffers, and hæmorrhages into it are common and widespread.

In the dog the heart's action is normally intermittent.

Foreign bodies in the heart of cattle, especially cows, are well known, and give rise to a peculiar train of symptoms. **Vegetations** on the valves of both the dog and pig are recognised in connection with certain infectious diseases.

CHAPTER III

THE BLOODVESSELS

THE use of the bloodvessels is to distribute the blood over the body, to bring it into contact with the tissues, and to return it to the heart. To accomplish this work there are arteries, capillaries, and veins.

The systemic **Arteries** arise from one common trunk, the aorta, which by the process of dividing and subdividing like the branches of a tree forms the arterial system. This system, measured by its total cross section, is very much larger than the parent trunk; in fact, its sectional area, and hence its cubic capacity, has been estimated as several hundred times greater.

The large arteries differ somewhat in construction from the small ones. The microscope shows that while the large vessels are principally elastic, the small ones are mainly muscular. This does not preclude the small vessels from exhibiting the elasticity possessed by the large ones, for muscular tissue is itself highly elastic.

This elastic property of arteries is an essential feature in their construction; it admits of a vessel stretching both in width and length, and at the same time insures its recovery to its original dimensions after the stretching force ceases to act. When we remember the intermittent force exercised by the left ventricle on the arteries, we have no difficulty in understanding the necessity for this elastic property. The arteries are always full; for example, in the horse during rest, every contraction of the left ventricle throws into them 1 litre (1·76 pints) of blood, which must be accommodated, and this is provided for by the distension of their walls. For every litre of blood entering the aorta, an equal amount must pass out at the periphery, and the reduction in the diameter of the vessels brought about by the exit of this fluid is due to the elastic recoil of the arterial wall. A further use of the elastic arterial wall will be studied when the flow of fluid through tubes is described.

Another essential feature possessed by arteries is their power of contractility. Just as the larger arteries are principally elastic, so the smaller ones are principally contractile. This contractility or power of reducing their diameter is produced by the muscular coat previously mentioned. Though the smaller vessels possess this muscular coat, it by no means follows that they are always fully contracted; in fact, special nerves exist for the purpose of supplying the needful impulses to the muscular tissue which controls or regulates the variations in the diameter of the vessels. In this way the contraction or relaxation of the muscular artery depends upon the set of nerves brought into operation; this movement of the smaller muscular vessels is a tap which regulates the blood-supply to any given part of the body.

Capillaries.—The minute arteries terminate in the capillaries, and the diameter of the capillary bed thus formed is calculated to be 800 times the diameter of the aorta. It is in these vessels that the interchange between the blood on the one hand and the tissues on the other takes place, and this is rendered easy by the fact that the wall of the capillary consists simply of a very thin membrane composed of cells known as endothelial plates. The capillary is capable of expanding and contracting, and so of accommodating more or less blood as the case may require; this is brought about by the elastic nature of the membrane composing the capillary wall (for there are no nerves supplied to them), under the influence of the varying internal fluid pressure.

The size of the capillaries varies; in places such as the lungs they are relatively large, in other parts such as the skin they are very small. Their size depends upon the amount of blood which has to pass through them; in consequence they are larger during active exercise than during rest. If they be observed microscopically in the living animal, the capillaries are seen as a network enclosing small islands of tissue. These are the areas where the interchange between the blood and tissues occurs. They represent the important part of the circulation, in spite of the fact that the longest capillary does not exceed a length of 0·5 mm. ($\frac{1}{50}$ inch), and that the blood is not contained within it for more than one second.

The **Veins** receive their blood from the capillaries. They are thinner walled than the arteries, and their walls collapse when they are empty. Though some degree of variation exists in their structure, yet, speaking generally, they contain less elastic and muscular material than arteries, and more fibrous tissue. In certain veins, such as the venæ cavæ and those of the pregnant uterus, there is a considerable development of muscular tissue in the walls.

The venous system is larger than the arterial, and its capacity is regarded as being two or three times greater. The abdominal veins are capable of holding the whole blood of the body, as may be seen, for instance, at post-mortem examinations. The veins as they pass from the capillaries towards the heart become reduced in number and increased in size, and they terminate in the right auricle of the heart by means of two trunks, the united areas of which greatly exceed that of the aorta.

In the veins valves are found. These are well marked in the veins of the head, neck, and extremities. The valves look towards the heart, and supply a simple and essential means of insuring the return flow of the blood along the veins to the heart. Certain veins have no valves, such as the large veins entering the heart, and those of the bones, abdomen, foot, and brain.

Veins are normally pulseless, but under certain conditions a pulse-wave may pass through the capillaries into the veins, producing a *venous pulse.* The best physiological example of this form of pulse can be experimentally produced by stimulation of the *chorda tympani,* a nerve supplying the submaxillary gland with fibres which cause the bloodvessels to dilate. Under stimulation the vessels dilate, the veins pulsate, and the blood coming from them is even arterial in colour. Another form of venous pulse is met with in the great veins at the root of the neck; the mechanism of the pulsation in these has already been explained (see p. 40). It is abnormal for pulsations to extend any distance up the jugular vein; when this occurs the explanation is pathological, not physiological.

Mechanics of the Circulation.—At each systole of the ventricle a certain amount of blood is forced under great pressure into an already full aorta, and imprisoned there by the closure of the aortic valves. The aorta dilates to receive this extra blood, because, owing to the friction in the smaller vessels, or, as we shall speak of it, the *peripheral resistance,* it is impossible for the amount pumped into the aorta at each systole to pass out at once at the periphery; in this way high blood-pressure is produced in the arteries. The increase in the size of the aorta to accommodate this extra blood commences near the heart, and runs as a wave to the periphery; this wave is the *pulse.*

The two important features of the circulation which we have now to consider are blood-pressure and pulse, and to understand these it is necessary that we should study briefly the laws which govern the flow of fluids through tubes.*

If water be pumped through a rigid tube or pipe, at every stroke of the pump as much fluid passes out at the farther end of the tube as enters it at the other. Between the strokes of the pump no fluid issues from the pipe; the jet is produced only at the moment the pump is in action. No more water can enter this rigid tube from the pump end than can leave it at the outlet. If water be now pumped through a *short* elastic tube, the outlet of which is in no way obstructed, the current of water through it behaves just as if the tube were rigid—viz., a stream of water issues from the outlet during the action of the pump, and nothing more happens until the next stroke. An important alteration can, however, be made to the current through the elastic tube by offering an obstruction at the outlet to the free passage of the water. The effect of this obstruction is that the elastic tube expands to accommodate the contents, while a stream pours from the partly obstructed outlet which no longer corresponds to the stroke of the pump, but is a continuous stream which issues so long as the pumping is continued. This continuous stream is produced by the elastic recoil of the tube keeping up the pressure which the pump imparted to the fluid, and the reason why the elastic recoil of the tube is now brought into play is the partly obstructed outlet, or, as we have already termed it, the *peripheral resistance.* If the elastic tube be of sufficient length, a continuous stream will issue in spite of the absence of an obstruction; this is brought about by the internal fluid friction against the walls of the tube, which of course causes a peripheral resistance. In elastic tubes, therefore, the recoil of the tube converts an intermittent into a continuous flow, and the distension of the tube which produces the recoil is caused by the *peripheral resistance.*

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* The subject of the movement of fluids in tubes is not only an extremely difficult branch of physics, but one still imperfectly understood. We have introduced less of it into this chapter than appears in most works on physiology, and, in fact, have touched only on those general principles which have a direct bearing on the circulation.

Whether in a living tube like a bloodvessel, or in a dead tube like a pipe, fluid flowing under a head of pressure meets with resistance; this is due to friction of the fluid particles against the wall of the tube. The amount of resistance is not the same throughout the length of the pipe; it steadily decreases to the exit; but this assumes that the pipe maintains an even bore throughout. If the pipe were to narrow at any point in its length, the friction would in consequence increase at that particular place. The resistance or pressure due to friction may be estimated at any part of the tube by the introduction of a gauge—viz., a vertical tube placed at right angles to the flow. In this tube the fluid will rise to a certain height, and the weight of the fluid column indicates the pressure exerted at that particular spot. Such a tube is known as a *manometer,* and the pressure it gauges is the *side* or *lateral pressure* due to frictional resistance.

Of the total force or head of pressure engaged in forcing fluid along a tube, the greater part is used up in overcoming the frictional resistance, the remainder imparts to the fluid a certain velocity, and the remaining pressure is known as the *pressure velocity*.

The whole mechanics of the circulation can be worked out on a model consisting of a syringe to represent the heart, elastic tubes to represent the bloodvessels, and a few clamps to offer the needful peripheral resistance. With such a model, if water be forced into the arterial tubes, the clamps being open and the peripheral resistance therefore very small, it is found, by means of a manometer, that the pressure in the arterial tube rises with each stroke of the syringe, and falls with the free pouring of the contents into the tubes representing the veins. As the peripheral resistance is small, the pulsation set up in the fluid readily passes into the veins, and a manometer will here register nearly the same rise and fall as in the arteries.

If, however, the vessels be clamped so as to produce a resistance, the first stroke of the pump causes the arteries to become distended; they then recoil, and while doing this they receive another stroke from the pump and become still more distended. Once more they recoil on their contents, and are once more distended by the action of the pump, and so on. If during this time the arterial manometer be watched, it will be observed that the mercury or water rises with each stroke of the pump, but instead of falling at once to zero as it did in the unclamped tube, it has time to fall only a short distance before a second stroke of the pump sends it still higher than before; this progressive rising is repeated at every stroke of the pump until the water or mercury refuses to rise any higher in the tube, contenting itself by rising to a certain height at each stroke of the pump, and falling to a certain level during the interval between one stroke and another. In other words, a mean pressure has been established in the tubes representing the arteries by the *peripheral resistance*, the elastic recoil of the tube, and the pumping of the syringe. So long as these factors remain the same the mean pressure will not vary. If, however, the clamped vessels be released, so as to allow fluid to flow more easily into the tubes representing the veins, the manometer at once shows a fall in the mean pressure owing to the removal of a certain amount of resistance, and by removing this resistance completely the mean pressure falls to zero. The *mean pressure*, then, represents the force which is necessary to cause as much fluid to pass through the periphery as is being pumped into the system of tubes by the syringe; if the peripheral resistance is high the pressure is high, and *vice versa*.

A careful study of this experiment places us in complete possession of the main facts of the circulation, but even now we have not learnt all the lessons it is capable of teaching.

If a manometer be placed on the venous side of the model, it will show a very low pressure at the time when the arterial pressure is high. If the arterial tubes be felt it will be observed that at each stroke of the pump they expand, producing what is known in living tubes as the *pulse;* this expansion of the tube is greatest nearest to the syringe, dying out entirely at the peripheral resistance. It is evident that, if we loosen the clamps and so reduce the resistance and lower the mean pressure, pulsatile waves will pass over to the venous side of the model, and these can be again obliterated by screwing up the clamp. Lastly, our model, if working at mean pressure, will show the effect of injury to the tubes; if the arterial tubes be pricked, a continuous jet of water shoots out, the strength of the jet varying with each stroke of the syringe, whilst an injury to the venous side produces no jet of water, but only a trickling flow.

Practically, this embraces our knowledge of the main facts of the circulation, for all we have found true of syringe, elastic tubes, and clamps, will be found true of heart, bloodvessels, and peripheral resistance. The heart has to keep the arteries full; the innumerable small arteries with their muscular coats supply the peripheral resistance. Under the influence of this and the contraction of the left ventricle, the pressure in the arteries rises so high, and their distension is so great, that as much blood passes through the periphery during the contraction of the heart and the ensuing pause as enters the aorta during the contraction of the left ventricle. The elastic nature of arteries insures that an intermittent is converted into a continuous flow, and thus a perpetual pressure is kept up on the mass of blood during the heart's pause. By a contraction of the arterioles the peripheral resistance is increased and the blood-pressure raised; by a relaxation of the arterioles the peripheral resistance is reduced and the blood-pressure falls. We have stated that a contraction of the arterioles by increasing the resistance raises arterial pressure and as a rule lowers that in the veins. This holds equally true for the pressure conditions in the vessels of any locally circumscribed area of the body as for the vascular system generally. It must not, however, be forgotten that local effects may and do produce general effects. If, for instance, *one* artery alone contracts, this must lead to an increase of arterial pressure, which produces an increased flow of blood through all the simultaneously uncontracted arteries and through these into the veins. When the contracted artery is small, so that the area it supplies is limited, the local effects are more marked than the general effects. If, on the other hand, the local area affected is at all large, the influence of changes in the arteries of this area on the general blood-pressure may be very obvious.

We shall meet with a striking instance of this when dealing with the action of the depressor nerve on blood-pressure, through the medium of alterations brought about by means of the splanchnic nerve, in the arteries which supply the splanchnic area.

Blood-Pressure.—From what has been said, it is hardly necessary to define blood-pressure as the pressure exercised upon the blood in the elastic vessels, resulting from the action of the heart and the peripheral resistance.

If the peripheral resistance is great through a contraction of the arterioles, the amount of fluid passing into the veins is reduced in quantity; a larger quantity of fluid will in consequence exist between the pump and its outlets, and the blood-pressure will rise. If, on the other hand, the blood is passing freely through the dilated arterioles, the blood-pressure falls. When the heart is more active, or when the arterioles contract, the blood-pressure rises; when the heart is less active or the arterioles dilated the blood-pressure falls.

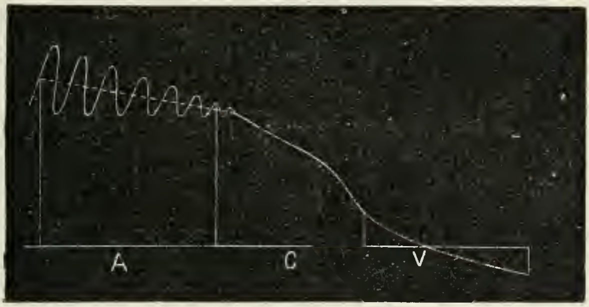

FIG. 27.—DIAGRAM TO ILLUSTRATE THE SLOPE OF PRESSURE ALONG THE VASCULAR SYSTEM (STEWART).

A, Arterial; C, capillary; V, venous tract. The interrupted line represents the line of mean pressure in the arteries, the wavy line indicating that the pressure varies with each heart-beat. The line of the veins passes below the abscissa axis (line of zero in atmospheric pressure), indicating that at the end of the venous system the pressure becomes negative.

The mean pressure in the arteries is highest close to the aorta and lowest in the region of the periphery; the fall in pressure from the aorta to the periphery is gradual. At the minute arterioles the fall in pressure is rapid; in the veins gradual and very slow; in fact, owing to causes to be dealt with in the chapter on Respiration, a negative pressure may exist in the great veins near the heart. Fig. 27 exhibits in a graphic form the fall in blood-pressure in the different regions of the vascular system.

It has been seen that the amount of side pressure exercised by fluid in a tube is ascertained by means of a manometer; precisely the same principle is employed to ascertain the side pressure in a bloodvessel, here called blood-pressure. It is interesting to observe that the first blood-pressure experiment ever performed was carried out on a horse, a vertical tube being placed in the femoral artery, in which the blood rose to a height of 8 feet 3 inches. It is, of course, for several reasons inconvenient to work with a long tube, and in consequence most manometers are U-shaped tubes containing mercury which is made to balance the pressure to be measured. The greater specific gravity of this metal enables a tube nearly fourteen times shorter to be employed. The inertia of mercury renders it useless for recording delicate or sudden alterations in pressure; these are obtained by means of spring manometers.

In Fig. 28 is shown the apparatus employed in determining blood-pressure with the ordinary mercury manometer.

The *Mean Arterial Pressure* is increased at each systole of the ventricles, and falls at each diastole; the maximum pressure is therefore known as systolic, the minimum as diastolic. In the aorta of the dog the systolic pressure may be 168 mm. (6¾ inches), the diastolic only 100 mm. (4 inches). The average of these two pressures is sometimes spoken of as the *pulse pressure* or *mean pressure.* The farther the vessel is situated from the heart, the less the difference between systolic and diastolic pressures, until finally in the capillaries there is no difference, and consequently no pulse.

In the aorta of the horse the blood-pressure may vary from 321 mm. to 150 mm. (12½ inches to 6 inches); in the dog, from 168 mm. to 100 mm. (6¾ inches to 4½ inches); in the sheep, from 206 mm. to 156 mm. (8 inches to 6¼ inches).

In the carotid of the horse the pressure is from 325 to 215 mm. (12¾ inches to 8 inches), equal to a column of blood 9¼ feet to 13¾ feet in height.

Neither size of body nor pulse-rate bear any relation to the amount of blood-pressure present in the arteries of an animal. The pressure in the carotid of the goose is nearly the same as in the carotid of the horse.

Influence of Muscular Work on blood-pressure is very marked; the pressure is raised because muscular contraction causes mechanical compression of the vessels of the muscles. Every movement of the body, every movement of a limb or part, affects the blood-pressure in it; in the large arteries the pressure will from this cause be found to be constantly varying, unless the animal be absolutely immobilised. There is also another important cause of variation—viz., the increased force and frequency of the heart-beat.

Effect of Gravity on Blood-Pressure.—L. Hill has demonstrated the influence on the blood-pressure of hydrostatic pressure due to gravity. He has shown in man that the arterial pressure is higher in the erect than in the horizontal position; that it is higher in the relaxed leg than in the arm to the extent of the column of blood separating the two points of measurement. Whether the body is placed in the horizontal, vertical, or inverted position, the blood-pressure in the arteries at the same level as the heart remains little altered, but in the vessels located below the heart the pressure is increased. Constant compensations are occurring in the circulatory system to guard against important alterations in blood-pressure due to gravity. These are effected by a varied output of blood from the heart, but especially by dila-

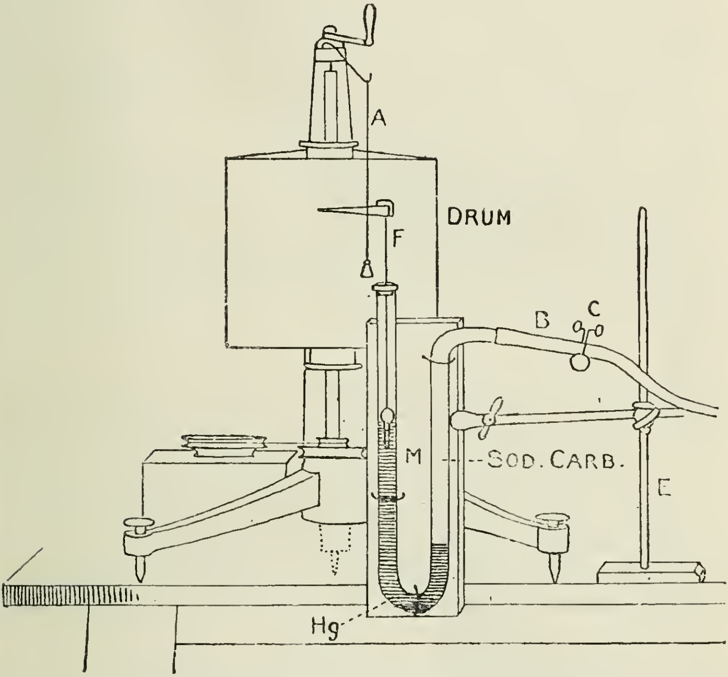

FIG. 28.—ARRANGEMENTS FOR TAKING A BLOOD-PRESSURE TRACING (STEWART).

M, Manometer; Hg, mercury; F, float armed with writing-point; A, thread attached to a wire projecting from the drum, and supporting a small weight. The thread keeps the writing-point in contact with the smoked paper and the drum. B is a strong rubber tube connecting the manometer with the artery; C a pinch-cock on the rubber tube, which is taken off when a tracing is to be obtained.

tation or constriction of the splanchnic area. Under abnormal conditions, such as ill-health, these compensations are absent or imperfect, and anyone who has been in bed for a few days, and then assumes the vertical position, knows the faintness which follows from the general fall in blood-pressure due to dilatation of the splanchnic area. If the ordinary hutch rabbit be held in the vertical position for a period varying from one-quarter to three-quarters of an hour, it will in all probability die. The cause of death is cerebral anæmia; under the influence of gravity the blood collects in the splanchnic area and the blood-pressure in the aorta falls. With a wild rabbit, dog, or cat, this experiment fails, the explanation being that the tense abdominal walls of the animal leading an active life compress the splanchnic area and prevent the blood collecting in the abdominal cavity. In a dog or cat previously poisoned by chloroform or chloral the experiment succeeds, as the tone of the abdominal walls is lost. When a horse rears up and falls backwards, it may be due to temporary cerebral anæmia resulting from want of compensation in a vertical position, apart from any question of loss of balance.

The arterial pressure varies, as has been said, with each systole of the ventricle, but besides this there are also certain larger and longer undulations obtainable in graphic records of blood-pressure which hitherto have been regarded by physiologists not as connected with the heart, but as caused by the movements of respiration. It has been observed that inspiration causes a rise and expiration a fall in pressure. This important action of the respiratory pump has never been quite satisfactorily explained, though we now have the view of T. Lewis, who finds that the rise of pressure on inspiration is due to the lessened pressure in the pericardium and consequent increased filling of the heart. If the pericardial sac be opened to the air, no such curves are produced. Lewis therefore concludes that the effect due to changes in the intrapleural pressure is produced entirely by the heart. The question will be again examined in dealing with respiration. The character of the curve produced is seen in Fig. 29.

The *Blood-Pressure in the Capillaries* is very difficult to ascertain. It is probably $\frac{1}{9}$ to $\frac{1}{7}$ of that in the large arteries, or lies between 20 to 40 mm. of mercury.

Hill compares the capillary system to a sponge, squeezed and filled continuously by the active motions of the body. The contents of the capillary vessels are constantly being pressed onwards by muscular movements, so that the pressure in them must be continually varying. Hill has shown in the human subject that in an arm held down, the fist being clenched, the pressure in the arteries and veins is high, but in the capillaries of the fist it is *nil*, owing to their compression.

Blood-Pressure in the Veins is $\frac{1}{14}$ or $\frac{1}{15}$ of that in the large arteries. The greater the distance the veins are from the heart, the greater the pressure, so that the highest pressure is in the peripheral veins and the lowest in the jugular. In a sheep the following values were obtained:

Jugular vein	0·2 mm.	($\frac{1}{100}$ inch).
Facial vein	3 ,,	($\frac{1}{8}$ inch).
Brachial vein	12 ,,	($\frac{7}{16}$ inch).
Crural vein	14 ,,	($\frac{1}{2}$ inch).

The venous pressure in a dependent part such as a limb is higher than in a part like the head and neck, where the venous flow is assisted by gravity. During work the venous pressure in the limbs rises, owing to the increased ventricular output, constriction of the abdominal veins, and compression of the veins of the limbs. A distended condition of the heart also causes the venous pressure to rise, owing to diminished intake.

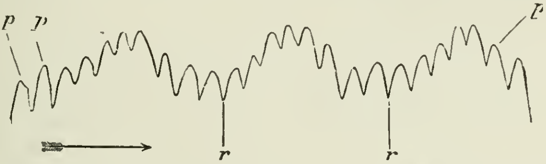

FIG. 29.—TRACING OF ARTERIAL PRESSURE WITH A MERCURY MANOMETER (FOSTER).

The smaller curves *P*, *P* are the pulse-curves due to the heart-beat. The space from *r* to *r* embraces a so-called respiratory undulation. The tracing is taken from a dog, and the irregularities visible in it are those frequently met with in this animal.

In the large veins just as they enter the heart the pressure is very low. The manometer may even at intervals show a negative pressure. In the anterior vena cava of the dog a negative pressure of -3 mm. ($\frac{1}{8}$ inch) may be registered. The negative pressure in the veins entering the thorax is due to the fact that the pressure within that cavity is below that of the atmosphere, so that an aspirating effect is produced upon the blood in these veins. It is this aspirating action which renders operations at the root of the neck in the human subject dangerous should air enter the wounded veins. Judging from the writer's experiments on the horse, blowing air into the veins causes no discomfort until a considerable amount has been introduced; even then only sighing respirations are produced.

Blood-Pressure in the Pulmonary System.—The variations in pressure in the pulmonary system are very much less than those occurring in the general circulation, and are believed not to exceed 15 to 20 mm. ($\frac{3}{4}$ inch) of Hg.

In the pulmonary artery the pressure is only about one-seventh of that in the aorta. This pressure decreases throughout the entire pulmonary channel up to the left auricle. The resistance offered by the pulmonary capillaries is less than the peripheral resistance experienced in the systemic circulation.

Influence of Hæmorrhage on Blood-Pressure.—The amount of blood which may be removed from the body without lowering the blood-pressure is surprising. This is explained by the fact that the vessels adjust themselves to the reduced amount of fluid in circulation. This adjustment is effected by means of a nervous apparatus to be dealt with presently, by which the blood-pressure is kept up. Experiments show that it is not until two-fifths of the blood in the body have been removed that the blood-pressure begins to fall; after cessation of hæmorrhage the pressure again rises, unless the loss of blood amounts to 3 per cent. of the body weight, in which case the low pressure becomes dangerously permanent.

Stewart's observations on dogs show that an animal may recover even after losing more than half its blood.

We have previously referred to the question of blood-letting. The boldness with which our forefathers used the lancet, especially those who believed in a heavy bleeding as a preliminary treatment, is justified by the physiological evidence above mentioned—viz., that it is not until about one-quarter of the blood in the body is drawn off that any effect on the blood-pressure is evident.

It is astonishing how rapidly a deficiency in the circulating fluid is made good, the fact being that, quite apart from the repair which is being effected through the thoracic duct, the tissues give up their fluid in an endeavour to replace the loss of blood. It is the loss of fluid by the tissues which causes the thirst of hæmorrhage.

Hill has shown that the effect on the blood-pressure of increasing the volume of fluid in circulation is very slight. The arterial pressure and the pressures in the venæ cavæ rise with the injection, but soon fall to the old level, the injected fluid being disposed of in the dilated venous reservoirs, especially those of the splanchnic area. Animals which have been transfused to the extent of 10 or 12 per cent. of the body weight—viz., more than twice the normal amount of blood—suffer from heart failure, the blood-pressure rising and falling as the overloaded heart does its best to cope with the difficulty. Excessive transfusion can best be borne if carried on slowly, in order that the large abdominal veins and those of the liver may be given time to accommodate the increasing bulk of fluid.

The influence of the nervous system on blood-pressure will be studied presently.

Circulation in the Living Tissues.—The circulation in the living animal may be easily seen in the web of a frog's foot, or in the mesentery of a mammal, and in this way we learn exactly how the corpuscles behave within the vessels.

In all capillary vessels of small size the corpuscles pass through singly, sometimes revolving in the plasma, traversing certain sections very rapidly, others very slowly. In the vessels larger than the capillaries, such as the commencement of the small veins, the stream of blood behaves somewhat differently; in each of these the centre of the vessel is occupied by a rapidly moving column of red cells, the *axial* stream, whilst between these cells and the coats of the vessel is a clear layer or zone, the *inert* layer, in which may be seen the white corpuscles strolling lazily along the sides, occasionally stopping, then moving forward once more. This difference in the behaviour of the corpuscles is due to the physical facts that the friction against the sides of the vessel is greater than in the centre, and that the red corpuscles, being heavier than the plasma, are drawn into the rapid part of the current. This also explains why the lighter leucocytes hug the walls of the vessel, through which, as previously pointed out, they may pass in order to gain the tissues without.

Under the influence of inflammation the slowly moving leucocytes attach themselves to the walls of the capillaries and venules, and pass into the tissues in large numbers. Small numbers of red corpuscles may also pass out. This process is known as *diapedesis*. Inflammatory changes are essentially due to the cell wall, and not to the blood, and this is proved by the fact that an artificial corpuscular fluid introduced into an inflamed area behaves exactly as does the blood.

The Pulse.—When the left ventricle contracts it drives a new supply of blood into an already full aorta, and room for it has to be found. This can be effected in one of two ways, either by displacing an equal volume of fluid already in the system, or by temporarily making the artery larger. The latter process is followed as being the more economical in energy. The aorta distends to receive the additional blood; this distension is followed by an elastic recoil of its walls which drives more blood along another segment of the vessel; this accordingly distends and then recoils, and so the process repeats itself in waves throughout the arterial system. This distension and elastic recoil is the pulse.

Each expansion of the arterial wall coincides with a contraction of the ventricle, and so each beat or throb of the pulse corresponds to a contraction of the heart. The rhythmical force of the heart is stored up in the arteries as elastic recoil; this intermittent expansion and contraction of the arteries gradually becomes less marked at a distance from the aorta, and dies out at the arterioles.

Attention has previously (p. 68) been drawn to the fact that the *elastic* properties of the arterial wall, together with the *peripheral resistance* in the smallest bloodvessels, convert the intermittent flow started by the heart into the continuous stream in the capillaries and veins. In seeking for the cause of the disappearance of the pulse, we find it similarly in the elastic property of the arterial walls. Each inch of the arteries is engaged, by means of its sudden distension after each heartbeat and its more gradual elastic recoil before the next, in sheltering the capillaries from the effect of that beat. The oscillations of pressure which give rise to the pulse are, so to say, 'damped' by the elastic arterial walls, or in other words converted into a steady pressure, a fraction of the pulse being thus actually destroyed by each inch of the arteries. When all the fractions thus destroyed are added together, we can readily understand why the initial 'jerk,' to which the pulse is due, has entirely disappeared just before it would otherwise have reached the capillaries. If the arterioles dilate considerably, when, in fact, less elastic recoil of their walls is called into play by the lessened peripheral resistance, it may be possible for the 'throb' to pass not only through the arterioles, but also through the capillaries, and to appear in the veins; in this way a venous pulse may be produced. An example of this has been given on p. 70.

The intermittent expansion of the arteries, called the pulse, travels from the aorta to the periphery, and produces a wave in the arterial system which is spoken of as the *pulse-wave.* From what has been said it is evident that the height of this wave is greatest nearest the heart, and falls to zero at the capillaries. The wave travels with considerable velocity, from 4½ to 9 metres (15 to 30 feet) per second. This may easily be determined by noting the interval between the commencing successive rises of two levers, resting consecutively on the wall of an artery, at a measured distance apart. The length of the pulse-wave is also considerable—viz., about 5½ metres (18 feet). This is arrived at by noting the time each single pulsation, travelling with the previously determined velocity, takes to pass completely under any *one* lever. Putting these data together, it is evident that the beginning of each pulse-wave is lost in the arterioles before its end has left the aorta.

No mental confusion should exist as to the difference, and the causes of that difference, between the velocity of the pulse-wave and the velocity of the onward flow of the blood. The factors which give rise to them are quite distinct. The pulse-wave runs along the surface of the blood-stream; the blood-current runs, as it were, within the pulse-wave; the former travels at a high speed, the latter comparatively slowly, at most some 381 mm. (15 inches) per second. The case is similar to that of a wave seen moving rapidly over the surface of a slowly flowing stream.

The pulse-wave can be studied by means of the graphic method; it is obvious that a lever placed on a pulsating vessel will be moved up and down, and may be made to trace a curve which will record the passage of the pulse-wave under the lever at that particular spot. A tracing thus obtained, known as a *sphygmogram,* simply registers the expansion and recoil of the artery while the wave is passing; it will not give a tracing of the pulse-wave itself, which, as we have seen, is 18 feet in length, but it gives the details of the *form* of the wave. It may be at once said

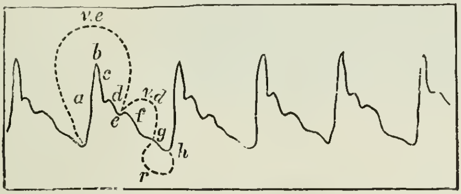

Fig. 30.—Normal Sphygmogram modified from Dudgeon; Pressure 2 Ounces (Hamilton).

v.e, The period of ventricular systole; *v.d,* the period of ventricular diastole; *r,* the period of rest; *a, b, c,* primary or percussion wave; *d,* first tidal or predicrotic wave; *e,* aortic notch; *f,* dicrotic wave; *g,* second tidal wave; *h,* termination of pause and beginning of ventricular systole.

that unless the proper degree of pressure is kept on the vessel, great irregularity in the sphygmograms will be produced, due to instrumental errors, and not to the true pulse-wave.

The simplest description of a sphygmogram (Fig. 30) is that it consists of a nearly vertical unbroken upstroke (the *anacrotic* limb), and an oblique downstroke (the *catacrotic* limb), which is broken by two or three waves known as *catacrotic waves.* Of these two or three waves *f* (Fig. 30) is one of the few which occurs with any regularity, and is known as the *dicrotic* wave. The notch *e*, described as the aortic notch, is caused by the closure of the aortic valves. The dicrotic wave is produced by a recoil of blood, the result of closure of the aortic valves; this reflected wave passes from the centre over the whole arterial system. The smaller waves in the catacrotic limb are either vibrations of the arterial wall, or reflections of the pulse-wave from the periphery towards the heart. That the dicrotic wave is a reflection from the aortic valves is shown by the tracing in Fig. 31, taken from the facial artery of the horse, *A* before, and *B* after destruction of the valves. In *B* the dicrotic wave has disappeared. A well-marked dicrotic pulse gives a double beat of the pulse for each single contraction of the heart (see Figs. 32 and 33). Venous pulse-tracings are referred to at p. 46.

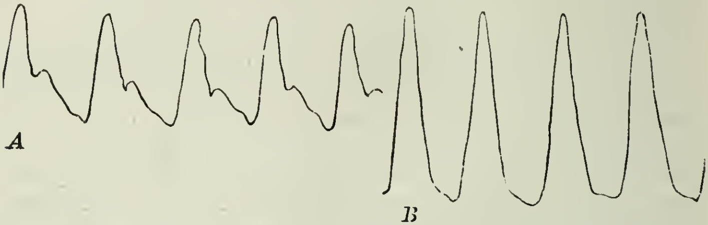

FIG. 31.—TRACING FROM THE FACIAL ARTERY OF THE HORSE (HAMILTON). *A*, before; *B*, after destruction of the aortic valves.

The pulse-wave distends all the arteries of a part, and by so doing actually increases the volume of any part or organ at the moment of its passage; this has been described as the **volume pulse**, and it can be recorded in the following manner: A limb, a kidney, or spleen, is placed in a closed chamber containing fluid; at each passage of the pulse-wave the volume of the part, being increased, causes an increased pressure in the fluid, and this, by means of any of the methods of registering changes of pressure in a fluid, may be made to furnish a graphic record. An instrument for this purpose is known as a *plethysmograph,* and in Fig. 34 the apparatus may be seen as applied to the arm. So sensitive may this method of registration be made, that a tracing of volume pulse may show not only every beat of the heart, but even the dicrotic wave (see Fig. 35).

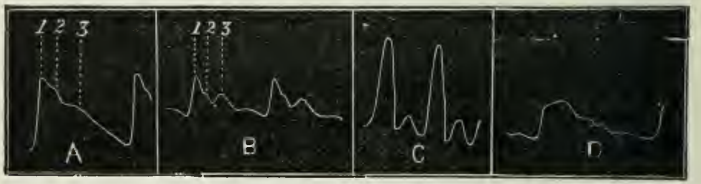

FIG. 32.—PULSE-TRACINGS (STEWART).

1, Primary elevation; 2, predicrotic or first tidal wave; 3, dicrotic wave. The depression between 2 and 3 is the dicrotic or aortic notch; 3 is better marked in B than in A. C, Dicrotic pulse, with low arterial tension; D, pulse with high arterial pressure, summit of primary elevation in the form of an ascending plateau.

In connection with pulses the term **tension** has been employed by pathologists; thus pulses of high and of low tension have been described, and an attempt has been made to distinguish between the pathologits's tension and the physiologist's pressure. If tension be defined as the elastic force exerted by the artery on the blood within, it is evident that this bears some distinct relation to the force distending the artery—viz., the blood-pressure; a high blood-pressure and high arterial tension describe the same conditions. In an artery giving a high tension the dicrotic wave is nearly extinguished; the vessels, in fact, are so full that the recoil wave makes very little impression on the tense arterial wall; when blood-pressure is low and the amount of movement in the artery great, the recoil or dicrotic wave is very marked (Figs. 32 and 33).

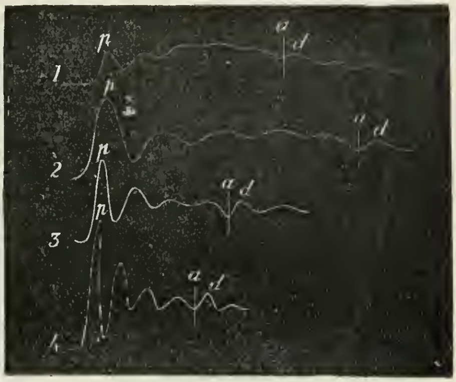

FIG. 33.—CURVES OF BLOOD-PRESSURE TAKEN WITH A SPRING MANOMETER FROM THE CAROTID ARTERY OF A DOG (AFTER HÜRTHLE).

When 1 was taken the blood-pressure was high; 2 corresponds to a medium; 3 to a low; and 4 to a very low pressure; *p* is the primary elevation. This and the succeeding elevations between *p* and *a* are called 'systolic waves.' The systolic waves are followed by a marked elevation, *d*, which corresponds to the dicrotic wave.

The pulse varies in character, according to age, condition, and state of the system; it also differs according to the class of animal. The following table shows the pulse-rate in different animals:

Elephant - - -	25	to	28	beats per	minute.
Camel - - - -	28	,,	32	,,	,,
Horse - - - -	36	,,	40	,,	,,
Ox - - - -	45	,,	50	,,	,,
Sheep - - - -	70	,,	80	,,	,,
Pig - - - -	70	,,	80	,,	,,
Dog - - - -	90	,,	100	,,	,,

Certain variations uniform in all animals occur in the pulse-rate. It is always much quicker in the young animal than in the adult. The heart of a foal at birth beats 100 to 120 per minute, and that of a calf 90 to 130 per minute. As the animal increases in age the pulse-rate drops, and in old age the pulsations are not only reduced in number, but are weaker.

The rigid condition of the arterial wall in old age alters the shape and nature of the pulse-tracing.

Between size of body and pulse-rate there is a distinct connection; it varies inversely as the height—in the elephant 27 beats a minute, in the mouse 670.

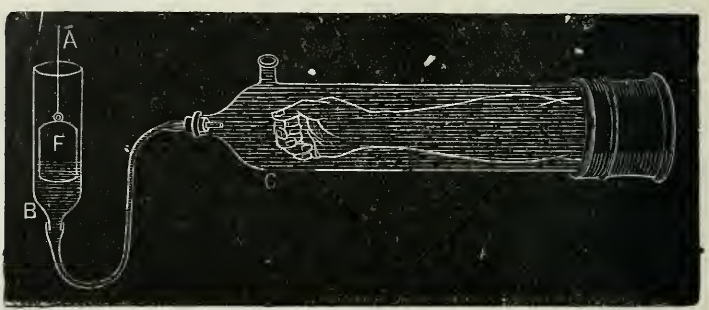

Fig. 34.—Plethysmograph for Arm.

F, Float attached by A to lever, which records variations of level of the water in B, and therefore variations in the volume of the arm in the glass vessel C. Or the plethysmograph may be connected to a recording tambour. The tubulure at the upper part of C is closed when the tracing is being taken.

The heart-rate is rapidly responsive to any outside influence, such as excitement or fear. A harsh word, fear, or timidity will cause the pulse of a nervous animal to register nearly double the number of beats of the heart. To sickness or injury the pulse is instantly responsive, and is one of the cardinal aids both in diagnosis and prognosis. Variations of pulse-rate follow as the result of work, so that a marked increase in the number of beats occurs; this means a larger amount of blood in circulation through tissues which are in a state of activity and consequently in urgent need both of repair and of flushing.

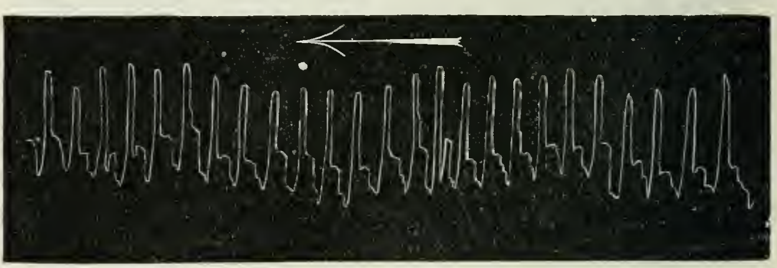

Fig. 35.—Plethysmograph Tracing from Arm (Stewart).

The tracing was taken by means of a tambour connected with the plethysmograph.

A relationship exists between the heart-rate and the condition of blood-pressure; when the blood-pressure becomes low, the heart-rate increases as the result of reflex stimulation, by which means the output of blood is increased. If the temperature of the blood be raised, the heart-beat increases in frequency, and there appears but little doubt that one cause of the increased pulse-rate in fevers is the actual temperature of the circulating blood. If the temperature of the blood be raised experimentally, it is found that a point is reached at which the heart ceases to beat; in the cat this has been found to be between 44° and 45 °C. (111° to 113° F.).

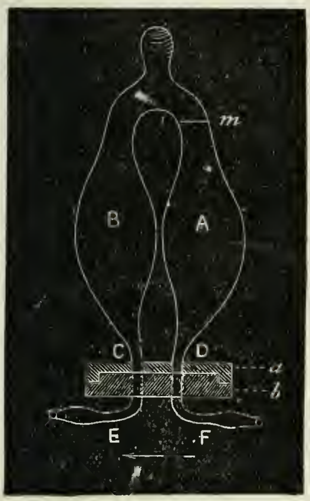

FIG. 36.—STROMUHR OF LUDWIG AND DOGIEL.

A, B, Glass bulbs; *a*, a metal disc, to which C and D are attached, and which can be rotated on the disc *b*; E and F, cannulæ attached to *b*, and connected with the peripheral and central ends of a divided bloodvessel; *m*, the mark to which the bulb is filled before rotation.

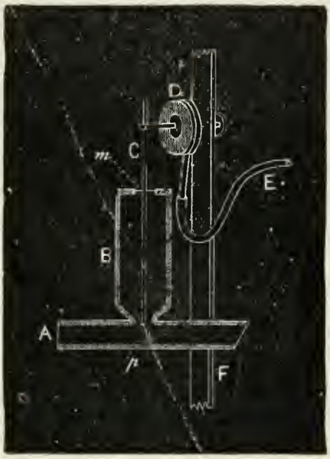

FIG. 37.—CHAUVEAU'S DROMOGRAPH.

A, Tube connected with bloodvessel; B, metal cylinder in communication with A. The upper end of B has a hole in the centre, which is covered by a membrane, *m*, through which a lever, C, passes. C has a small disc, *p*, at its end, which projects into the lumen of A, and is deflected in the direction of the blood-stream through A. The deflection is registered by a recording tambour, D, connected with the lever C, and transmitted by E to a drum.

The **Velocity of the Blood** varies in the arteries, capillaries, and veins, being greatest in the former, least in the capillaries, and rising again in the veins.

The velocity of flow is inversely as the sectional area of the tubes; the total sectional area of the capillaries is greater than that of the aorta, therefore the velocity is reduced; from the capillaries to the heart the area becomes smaller and the velocity increases.

The velocity of blood-flow depends on the width of the bed formed by the vessels; as the arterial system expands the velocity diminishes; in passing through the capillaries with their immense network the velocity is at a minimum; in passing towards the heart the vessels are reduced in number, hence the bed is smaller, and the velocity accordingly increased. The causes of the flow throughout the entire system are the contraction of the left ventricle, and the gradual fall in pressure which occurs from the aorta to the right auricle.

The vascular system has been compared to two cones placed base to base, the apex of one being the left ventricle, of the other the right auricle; where the bases of the two cones meet is the capillary network. The sectional area of this has been estimated by Volkmann as 800 times greater than that of the aorta, while, owing to the width of the bed, the rate of the passage of blood through it is 800 times slower than in the aorta.

Several ingenious instruments have been devised for the purpose of measuring the velocity of the blood. One, introduced by Ludwig, known as the *stromuhr* (Fig. 36), consists of a bulb of known size, and the length of time taken to fill this bulb of known capacity gives the velocity. The *dromograph* of Chauveau (Fig. 37) is employed for a similar purpose. It consists of a tube placed in the course of the vessel; within the tube is a plate; the blood streaming past this plate deflects a needle, and the angle of deflection may be expressed in terms of velocity.

By means of these appliances the following velocities have been obtained in the vessels of the horse:

Carotid artery: 30 to 40 cm. per second (11·8 to 15·75 inches).
Metatarsal artery: 5·5 cm. per second (2·2 inches).
Jugular vein: 22 cm. per second (8·85 inches).

The velocity in the larger vessels is not constant; it is greater during systole and less during diastole. Chauveau obtained the following result in the carotid of the horse:

During systole: 52 cm. per second (20·47 inches).
Beginning of diastole: 21·75 cm. per second (8·66 inches).
During the pause: 15 cm. per second (5·90 inches).

The mean velocity in the carotid of the dog is 26·5 cm. per second (10½ inches).

At the end of systole: 30·5 cm. per second (12 inches).
At the end of diastole: 21·5 cm. per second (8½ inches).

The difference between systolic and diastolic velocities becomes less and less as the small arteries are approached, until finally it disappears. We may say, therefore, that the velocity is more uniform in the small than in the large arteries.

The velocity of the blood is not as great as at first sight appears. If the stream in the carotid of the horse were never to diminish in velocity, it would cover nearly one mile in an hour.

The velocity of the blood in the arteries farthest from the heart is less than in those nearest the heart; for example, in the above table a horse with a carotid velocity of 30 to 40 cm. per second had a metatarsal velocity of only 5·5 cm. per second.

In the capillaries the velocity is very low, perhaps not more than 0·5 to 1 mm. ($\frac{1}{32}$ to $\frac{1}{16}$ inch) per second. This reduction, as we have seen, is due to the width of the bed through which the fluid is flowing. As the veins are reached and the bed narrows, the velocity increases, until the heart is approached, when the velocity in the veins, though increasing, is still much less than that in the corresponding arteries. A horse with a carotid velocity of 30·5 cm. (12 inches) gave a jugular velocity of 22·75 cm. (9 inches). It is generally considered that the velocity of the blood in the large veins entering the heart is about half as great as that in the aorta.

During work the velocity in the vessels increases. The flow of blood through the carotid of the horse has been observed by Lortet to be five or six times greater during the time the animal is feeding than when at rest.

In speaking of blood-pressure we drew attention to the fact that when the heart is more active, or the arterioles contract, the blood-pressure rises, and that when the heart is less active, or the arterioles dilate, the blood-pressure falls. These factors also affect velocity. When the heart-beats increase in force, the velocity of the blood is increased; when they are diminished, the velocity is reduced. Further, it is obvious, from what has been said of the influence of the width of the vascular bed, that if the arterioles dilate the velocity of the blood through the capillaries is increased, and if they contract it is diminished.

In the pulmonary circulation the circulation time is much shorter than in the systemic, only one-fifth or one-sixth of the time being required for a lung circuit as compared with a long body circuit.

Any attempt made to estimate the velocity of the blood by dividing an artery, and measuring the escape of blood from its cut end in a given time, would lead to erroneous conclusions, for the velocity in a closed artery and an open one are two different things. In the undivided artery the peripheral resistance reduces the velocity; in the divided artery the peripheral resistance largely disappears, and the velocity is five or ten times greater, so that the carotid of a horse does not bleed with a velocity of 16 inches per second, but of nearly 160 inches per second. Or, to put it in a practical way, if the carotid of the horse has a sectional area of 0·2 square inch, the amount of blood passing through the unwounded vessel amounts to 2 ounces per second, while if the same vessel be divided the loss of blood would be nearly 1 pint per second.

The **Duration of the Circulation** depends upon the length of time it takes a red corpuscle to travel from a given point and back to it again.* But there are many different paths it can take. For instance, from left heart through coronary vessels to right heart and again back to left heart would occupy a shorter time than a course through the liver, or through the feet or tail, so that a circulation time may mean nothing more than that a certain number of corpuscles have found the shortest cut through the circulation, or, on the other hand, have taken the longest. In a horse with a pulse frequency of 42, the average complete circuit is performed in 31·3 seconds (Hering), equivalent, according to this observer, to about 28 beats of the heart. In the rabbit with a pulse frequency of 168 per minute, the time occupied in completing the round of the circulation was 7·79 seconds, or, again, 28 heart-beats; in the dog 16·7 seconds, or 26·7 heart-beats.

Stewart, who introduced the method of electrical conductivity for ascertaining the duration of the circulation, states that the time occupied by the blood in passing through the kidney, spleen, and liver is relatively long and much more variable than that required for a circuit of the lungs. In a dog weighing 13·3 kilogrammes the average circulation time in the spleen was 10·95 seconds, in the kidney 13·3 seconds, in the lungs 8·4 seconds. The same observer found the circulation time of the stomach and intestines of the rabbit to be comparatively short, not exceeding that of the lungs. The retina and coronary vessels of the heart had the shortest time circulation.

Influence of the Nervous System.—It is only during the last sixty years that the existence of a set of nerve fibres governing the calibre of the bloodvessels has been known. C. Bernard observed that in the cervical sympathetic of rabbits there were fibres which on stimulation produced constriction of the bloodvessels of the ear; later he found a set of fibres which on stimulation produced a dilatation of the bloodvessels.

The control of the nervous system over the bloodvessels consists of these two actions—viz., dilatation and constriction; the nerves inducing the former are called *vaso-dilators*, and those bringing about the latter *vaso-constrictors*. Collectively these nerves are known as *vasomotor*. The vaso-constrictor fibres act by causing contraction of the muscular coat of the arterioles. The capillaries are not affected; in fact, as far as is at present known, there is no vasomotor supply to capillaries. The vaso-dilators act by relaxing the muscular coat of the arterioles.

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* The circulation time is determined either by injecting an easily distinguishable salt into the blood, or with greater precision by increasing the electrical conductivity of the blood by injecting into it a neutral salt solution.

From what has been previously taught it is evident that a high blood-pressure is an essential condition throughout the life of an animal; whether awake or asleep, at work or at rest, a constant watch has to be kept over the vessels of the body, in order to produce not only an effective, but a purposeful circulation, for it is evident that the blood-supply to an organ in active secretion must be greater than when the organ is at rest. The nervous system is charged with the duty of controlling the bloodvessels and of regulating the blood-supply to them.

The system of nerves governing the bloodvessels is not under the control of the will, but belongs to that portion of the nervous apparatus generally known as the sympathetic. The sympathetic system has its origin in the brain and spinal cord; it is specially charged with functions relating to plain muscular tissue, cardiac muscle, and glands, so that the plain muscle constituting one of the coats of the arterioles comes under its control. The two opposite changes in the bloodvessels—viz., contraction and dilatation—are not caused by the action of the same nerve fibres. The constrictor nerves operate through the elaborate and complex system to which they belong—viz., the sympathetic; but the dilator fibres accompany cranial and spinal nerves, and may or may not have any connection with the sympathetic system, being included, however, in the larger system—the so-called autonomic (Langley).

The **Constrictor Fibres** originate in the medulla at a special part known as the **vasomotor centre.** The fibres from this centre pass down the spinal cord to end probably around the nerve cells in the intermedio-lateral column of the thoracic region. From these nerve cells medullated nerve fibres pass out in the inferior roots of the spinal nerves, and, leaving the latter by the white **rami communicantes**, join the lateral sympathetic chain, in which they run either forwards or backwards, depending upon the place of origin of the grey rami communicantes which supply the spinal nerves with their vasomotor fibres.

Those fibres which supply the vessels of the head and neck pass forwards to end in the superior cervical ganglion from which the non-medullated nerve fibres supplying the arterioles arise. The fibres for the bloodvessels of the limbs pass to the vertebral ganglia from which the non-medullated post-ganglionic fibres pass to the nerves of the axillary and sacral plexuses. Those for the skin of the trunk pass by the corresponding spinal nerves, while those for the abdominal viscera leave the vertebral chain of ganglia by the greater and lesser splanchnic nerves to end around certain prevertebral ganglia in the abdomen from which the non-medullated post-ganglionic fibres arise.

The essential feature in all these constrictor fibres is that they originate in the brain or cord, leave the latter as medullated nerves, and enter a sympathetic ganglion, where they terminate by arborising around cells in the ganglion. From these cells new fibres arise, which leave the ganglion as non-medullated nerves, and proceed to their destination either direct, as to the head, neck, and viscera, or through the spinal nerves.

If the spinal cord be divided below the medulla, and life maintained by means of artificial respiration, the immediate effect of division is a great fall of blood-pressure, due to dilatation of the bloodvessels; in the dog it will drop two-thirds below the normal The effect of division has been to cut off the constrictor influence, which was evidently issuing from some point above the section.

If in another animal the section be made above the medulla, no effect is produced on the blood-pressure. Evidently, therefore, the medulla contains a centre presiding over the important functions of maintaining the bloodvessels in the partially contracted condition known as *tone*, and it can readily be shown that this centre lies in the region of the fourth ventricle, and is only a few millimetres in length and still fewer in breadth. To this small area the name **vasomotor centre** has been given.

This centre, we have learnt, must be kept in a constant state of activity. This is effected, though perhaps not entirely, by the constant flow of impulses from the periphery to the centre. Impulses passing to a centre from without to within are known as *afferent*, those passing out from a centre to the periphery are spoken of as *efferent impulses*, and a collection of nervous matter where afferent impulses are received and efferent discharged is known as a *reflex centre*.

The afferent impulses which govern the centre in the medulla are carried to it through the spinal nerves from areas such as the skin and abdominal viscera, for these are the two great vascular areas which maintain and regulate the blood-pressure. On entering the superior root of the spinal nerves, the fibres travelling up the cord by means of collateral branches make connection with the vasomotor centre in the medulla. We have now seen the channels by which this almost microscopic collection of cells in the medulla is brought into connection with the vessels of the whole body.

The impulses carried by afferent fibres to the vasomotor centre are of two antagonistic kinds; they either stimulate it and produce contraction of the bloodvessels, with a consequent increase in blood-pressure, or they diminish the tone of the centre, produce a relaxation of the bloodvessels and a fall in pressure. The first fibres are known as **pressor,** the latter as **depressor,** terms which correspond to the effect they produce on the blood-pressure.

As previously stated, it is in the skin and abdominal viscera that the impulses which regulate the maintenance of normal arterial pressure originate; there are supplemental sources, but the above are the most important. The fibres passing from the skin area are stimulated by the external temperature, a low temperature causing impulses to be transmitted which contract the vessels, a high temperature causing a relaxation of the vessels, accompanied by congestion of the skin. But the splanchnic area is even more actively important than the skin in regulating blood-pressure, especially in those animals such as the herbivora, where the alimentary canal is largely developed. If the splanchnics be cut, the intestines become congested in consequence of dilatation of the bloodvessels, and there is a severe fall in blood-pressure. If the peripheral end of the divided nerve be stimulated, the vessels contract, and the blood-pressure at once rises.

The action of the constrictor fibres of the bloodvessels is always more in evidence than that of the dilators, and the reason of this can be readily understood by remembering that the arterioles have always to be kept in a condition of contraction if blood-pressure is to be maintained.

Bernard's classical experiment of dividing the cervical sympathetic in the rabbit produces not only a remarkable picture of vasomotor effects, but illustrates the constrictor impulses which are constantly passing to the bloodvessels. On division of the sympathetic, the ear on that side suddenly becomes flushed with blood, hot, and congested, and vessels not previously visible to the naked eye now become very apparent. If the upper end of the nerve be stimulated, so as to imitate roughly the impulses passing along it in an intact condition, the vessels at once contract, the flushed appearance disappears, and the ear becomes cooler.

Since, in the above experiment, mere severance of the nerves which connect the bloodvessels with the central nervous system leads to a dilatation of the arterioles, it is evident that impulses are, under normal conditions, being continually sent out along the nerves from the vasomotor centres. These impulses keep the arterioles normally in that state of medium or partial constriction which has already been described as arterial 'tone.' Now, inasmuch as the function of the vasomotor nerves is to regulate the blood-supply to any given area of the body, in exact accordance with the varying needs of that area, 'tone' becomes a factor of the utmost importance in this regulative mechanism. Without it all the arteries of the body would, in the ordinary passive condition of rest, be dilated to their full extent; hence no increased supply of blood could be provided except by an augmented activity of the heart, which would, of course, affect the body as a whole, and not any one limited part of it. 'Tone' insures that an arteriole will both dilate and contract, according as it receives less or more of the continuous constricting impulses, and thus the regulation of a varying blood-supply is made extremely perfect.

If the sciatic or brachial nerve be divided in the dog, as a rule the constrictor influence over the bloodvessels of the limb is lost, the foot-pads flush, and the feet rise in temperature. If the central end of the divided sciatic be stimulated, it is generally followed by a contraction of the bloodvessels and a rise in pressure. Occasionally the tone of the centre in the medulla is not raised, but reduced, and dilatation of the vessels and a fall in blood-pressure results. This experiment suggests that most afferent nerves, such as the sciatic, carry both pressor and depressor fibres, and that the effects which follow experimental stimulation depend upon whichever set of fibres is most efficiently stimulated (Fig. 38).

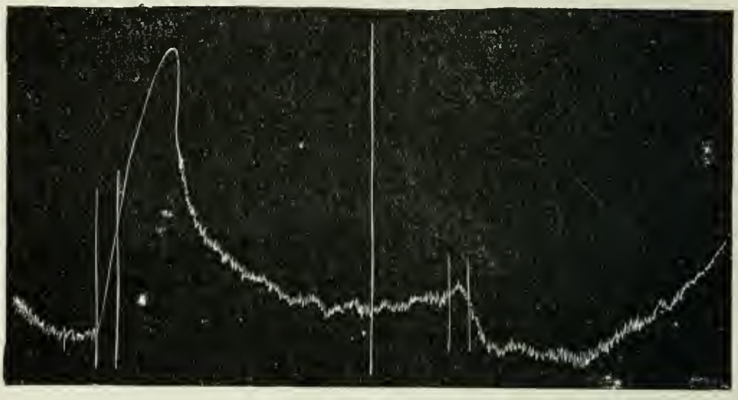

FIG. 38.—PLETHYSMOGRAMS: HIND-LIMB OF CAT (AFTER BOWDITCH AND WARREN).

To be read from right to left. On the left hand is shown the effect of slow stimulation of the sciatic (1 per second); on the right hand the effect of rapid stimulation (64 per second). In the first case the limb swelled owing to excitation of the vaso-dilators; in the second it shrank through excitation of the vaso-constrictors.

The best example of a depressor nerve is one we have already studied under that name (p. 60); it is the only peripheral nerve the stimulation of which invariably reduces blood-pressure. This nerve, it will be remembered, is capable of regulating the work of the heart by taking off strain through the medium of the abdominal venous cistern. Stimulation of the depressor acts like division of the splanchnic—viz., the abdominal vessels fill with blood and the blood-pressure falls.

Experimental inquiry shows that, in spite of the enormous importance of the vasomotor centre in the medulla, if the cord be divided in the lumbar region the vessels of the hind-limb dilate and the blood-pressure falls, but if the animal be kept alive the blood-pressure probably returns to the normal, though it is once again lost by destroying the already divided cord. These results are explained by saying that the cord possesses **vasomotor subcentres,** and that, given time, these are capable of carrying on the work unaided. It is even possible to carry the inquiry a stage farther, and by destroying all nervous connection, isolate the vessels from their innervation; even then the vascular tone may be recovered, and it is supposed that it is developed in the wall of the vessel itself, possibly in response to the stimulating influence of variations of the internal blood-pressure.

It is possible that the nature of the stimulus conveyed by afferent nerves to the vasomotor centre may determine the nature of the reflex which follows, and this is considered probable because the electrical stimulation of muscle always produces a rise in blood-pressure, whereas the mechanical stimulation by rubbing always causes a fall. The effect of stimulating the divided sciatic was recently referred to as producing constriction of the bloodvessels and a rise in pressure; but if the sciatic nerve be cooled and then stimulated, exactly the converse effects are produced—viz., a dilatation of the arterioles and a fall in pressure. Not only are the results obtained dependent on the nature of the stimulus, but the state of the centre itself is of the utmost importance in determining the results of reflex vasomotor stimulation. When an animal is deeply under the influence of chloroform or chloral, the functions of the vasomotor centre appear to be reversed, and excitation of *pressor* fibres causes a fall instead of a rise in pressure. If the centre be under the influence of strychnine, stimulation of the depressor nerve, instead of causing a fall in the general blood-pressure, produces a rise.

The vasomotor centres, both in the medulla and cord, are extremely sensitive to the varying amounts of carbon dioxide in the blood, and in this way they are believed to be capable of a good deal of self-regulation apart from the afferent impulses which flow in to their aid. An increased venous condition of blood leads to a constriction of the arterioles and a raising of the blood-pressure. In asphyxia the arterioles remain constricted under the influence of the intensely venous blood as it stimulates the vasomotor centre to unwonted activity, and though the initially high blood-pressure subsequently falls to zero, it does so, not because the arterioles have relaxed, but because the heart has failed.

It has been supposed that one cause of surgical shock is a deficiency of carbon dioxide in the blood. The prevention of this complication by avoiding a too free ventilation in the lungs, and so maintaining a carbon dioxide blood-pressure, has been recommended as a means of combating shock. The alarming depression which after a prolonged operation not infrequently follows the removal of the closed chloroform mask employed in chloroforming horses is doubtless due to the fall of blood-pressure caused by less CO_2 circulating in the vasomotor centre.

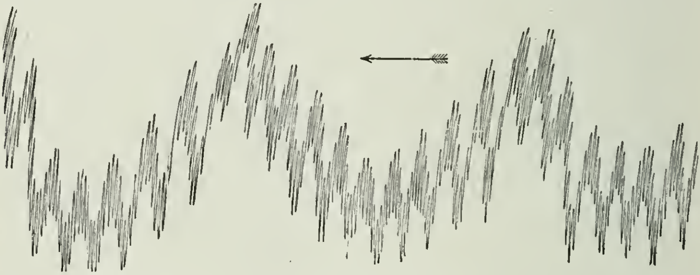

Fig. 39.—Blood-Pressure Curve of a Rabbit recorded on a Slowly Moving Surface to show Traube-Hering Curves (Foster).

The heart-beats are the closely situated up and down strokes, readily seen by means of a lens. The next curves are those generally regarded as due to respiration, the large bold undulations being the Traube-Hering curves. In each Traube-Hering curve there are about nine respiratory curves, and in each respiratory curve about nine heart-beats.

Rhythmical Activity of the Vasomotor Centre.—Under certain conditions, such as asphyxia and hæmorrhage, the vasomotor centre transmits to the vessels rhythmic constrictor impulses, which result in the appearance, on a simultaneous record of blood-pressure, of undulations known as Traube-Hering curves (Fig. 39). They can, of course, only be detected by taking a tracing of the blood-pressure. The existence of these waves is indicative of abnormal excitation of the vasomotor centre.

The Dilator Nerves.—Hitherto we have mainly dealt with the constrictor influence exercised over the bloodvessels, but the nervous system likewise produces a *dilator* effect. In contrast to the constrictor influence, the dilator is not *tonic* in its action. It might be supposed that a dilator effect would naturally follow as the result of removing a constrictor influence from a vessel, without the intervention of a separate or antagonistic nerve supply; and this is exactly what does happen in most cases. But it is equally certain that special vaso-dilator nerves exist, of which the *chorda tympani* is one of the best examples. This nerve supplies the bloodvessels of the submaxillary gland with dilator fibres; if the nerve be cut no evident change in the bloodvessels occurs, but if the end in connection with the gland be stimulated the vessels dilate, the arteries throb, and the blood passes through the gland with such rapidity that the venous blood becomes arterial in appearance. Much the same phenomenon occurs when the *nervi erigentes*, through which erection of the penis is produced, are brought into activity. If these nerves be divided there is no effect, but if the peripheral end be stimulated the organ swells as the result of its enormously increased blood-supply, and the blood flowing through the dorsal vein may now be fifteen times greater in amount than in the quiescent condition.

Though it is clearly established that true vaso-dilator nerves exist, there is still great difference of opinion as to the extent of their distribution. In most peripheral nerves, such as in the nerves of the limbs, both dilator and constrictor effects may, as has been mentioned, be obtained on stimulation, rapid induction shocks bringing about constrictor effects, slower shocks producing dilator effects. If the nerve—say the sciatic—be divided, the subsequent degeneration which follows affects the constrictor fibres earlier than the dilator. There is good reason for believing that the view originally held regarding muscles possessing dilator fibres may have to be modified in the light thrown on the matter by Bayliss, who has shown that there are fibres in the superior roots of the cord, where the axillary and lumbar nerves come off, which on stimulation produce dilatation of the vessels of the limbs. As these fibres are running from the limbs into the cord, difficulty has been experienced in explaining why stimulation should cause an impulse to travel in a direction opposite to the normal. However, the only explanation at present offered is that the fibres act in a double capacity, conveying to the cord sensory impulses from the limbs, and by the same fibres conveying efferent or outgoing impulses from the cord to the vessels, resulting in their dilatation.

The dilator nerves in their distribution—and we here refer to those whose existence is undoubted—are very different from the constrictor fibres. They leave the brain or cord by any cerebrospinal nerve, and may or may not pass into a sympathetic ganglion before distribution. In contrast to the constrictors, they pass direct to their destination instead of taking a roundabout course, and they do not lose their medulla until near their termination. There is no positively known centre in the medulla governing the vaso-dilator fibres. There is, however, undoubted evidence of such a centre in the cord, for erection of the penis will still occur as a normal reflex after the cord has been divided above the lumbar region.

All the 'depressor' influences exercised on the circulation are not produced through inhibition (withholding) of constrictor impulses. Some must occur through stimulation of dilator nerves, but of this subject very little is positively known.

It is evident from what has been said that the knowledge of dilator nerves for the body tissues generally is still in a very uncertain condition.

We have seen the general effects produced by vaso-constrictor and vaso-dilator nerves, and indicated some of the gaps which exist in our knowledge. The main features of the theory appear to admit of no doubt. The size of the vessels has to be automatically regulated according to the demand made for blood, so that a double set of fibres is provided, one to constrict and one to dilate them. A general contracted condition of the vessels must be maintained if the circulation is to continue; consequently, constrictor impulses appear always more in evidence than dilator. These constrictor effects are assisted by the contractile reaction of the arterial wall, the peculiar property of smooth muscle, and this contractile reaction is brought into play, even apart from nervous impulses, by the thrust given to the blood at each contraction of the heart. Substances circulating in the blood, the secretion of such glands as the adrenals, of which we shall learn more presently, act on the nerve plexus in the walls of the bloodvessels, causing them to contract and raising the pressure. The heart centre in the medulla is being constantly informed of what is occurring in the two vast systems —skin and splanchnic—which between them regulate the blood-pressure of the body. Equally, impulses are constantly streaming out from this centre to the vessels, some of a constrictor, others of a dilator nature, resulting either from the afferent impulses received or from the changes in the composition of the blood circulating through the medulla itself.

Absence of Vasomotor Nerves.—Some vessels have no vasomotor nerves. They have not been satisfactorily demonstrated in the vessels of the heart, nor in those of the lungs or brain. They are not found in veins (excepting the portal, which is really an artery), and are only provisionally accepted as occurring in muscles. If muscles possess vasomotor nerves, they must be essentially dilators, and it is easy to understand that these fibres may be brought into operation when the muscles contract, and thus provide a flow in proportion to the activity of the part.

It has, however, been suggested that the dilatation in the bloodvessels of muscles during activity may be due to the chemical action of acid metabolic products on the vessels themselves.

Surgical Shock.—The condition known as shock, which follows certain operations, is intimately connected with the vasomotor apparatus. This has been suggested in speaking of the influence of carbon dioxide in the blood in maintaining blood-pressure. In surgical shock there is a marked depressor effect on the circulation, and a falling blood-pressure is one of the earliest indications of its onset. The maintenance of blood-pressure is the cardinal principle in combating shock, yet the physiologist does not regard shock as beginning, as has been suggested, in the vasomotor centre, in consequence of the violence of sensory stimulation, but as originating more probably in the paralysis of the nervous connections with that centre. The cutting off of the afferent impulses which stimulate the vasomotor centre is the initial move towards the production of shock.

Aids to the Circulation.—The distribution of the blood-supply in accordance with the requirements of the various organs is the special duty of the system of nerves we have been studying. The requirements vary from time to time, even from moment to moment. Active digestion diverts the blood to the splanchnic area; active work causes the stream to pass into the muscles, and later into the skin, in order to get rid of the excess of heat. Some glands, such as the kidneys, are secreting constantly; others, like the pancreas, intermittently. A failing heart requires more blood, one struggling against an ever-increasing load requires less, and so on. Throughout the whole life of the animal this delicate balance has to be maintained, and it is effected by means of the nervous system acting through the medium of the heart and bloodvessels.

It is impossible in connection with this question of an efficient circulation to avoid once more referring to the heart, and it is impossible to avoid being struck by the close similarity of the nervous arrangements for the care, management, and control of these two communicating systems—heart and bloodvessels. The nerve fibres which constrict the bloodvessels, and those which cause a more forcible contraction of the heart, are of the non-medullated variety. They excite muscular action and increase wear and tear. The fibres which dilate the bloodvessels, and those which slow the heart, are both medullated, muscle-restraining, and exciters of repair rather than of disintegration. The impulses affecting heart and bloodvessels pass from the periphery to the centre—viz., they pass from skin and muscle, viscera and glands, and even from the heart and bloodvessels themselves, to the nerve centres presiding over these two important systems.

They are true reflex effects, and without these impulses the centres themselves are powerless to effect regulation.

The delicacy of the balance must not be displaced. The body does not consist of a set of isolated functions working in sequence; three or four or a dozen may be in operation at the same moment, and to each of these a full blood-supply must be guaranteed for so long and no longer than is necessary, or in such reduced or increased quantity as may be needed. Whether the animal be awake or asleep, this remarkable give and take, this perfect adjustment to all requirements, is taking place from birth to death.

There has been reason to think that a certain amount of self-help has been obtained from the tissues themselves. For instance, the lactic acid and carbon dioxide formed during muscular activity may cause dilatation of the vessels and an increased blood-supply. This chemical help has for some time been recognised, but it is only within recent years that we have learnt that the body is capable of elaborating substances which, when introduced into the blood, greatly affect the calibre of the blood-vessels and the rhythm and tone of the heart itself.

The Chemical Stimulus in Blood-Supply.—The study of the so-called ductless and functionless glands of the anatomist has given us one of the romances of physiology. The adrenals and pituitary bodies—tissues so insignificant in size that it was but rarely that more than a glance was given them during dissection—are known to furnish to the blood-stream chemical substances of the utmost importance to the circulation.

An extract of the medulla of the adrenals, when introduced into the circulation, increases the rhythm, force, and tone of the cardiac muscle (see p. 62), strongly stimulates the contraction of the arteries, except those of the heart, and causes a consequent great rise in blood-pressure. There is evidence that the internal secretion of the adrenals finds its way into the blood, for a larger amount of pressor substances may be recovered from the blood leaving an adrenal than from ordinary blood. Removal of the glands is followed by great weakening of the heart and a low blood-pressure; fatal results ensue.

Extracts of the posterior lobe of the pituitary body introduced into the circulation greatly increase the tone, but not the rhythm, of the heart muscle (see p. 62), and, with the exception of those of the kidney, cause constriction of the arterioles of the body. This gland also secretes a depressor substance which diminishes the force of the heart and permits the vessels to dilate. The extract obtained from the pituitary body under experimental conditions contains much less of the depressor than of the pressor substances, but it may well be that under physiological conditions they are passed into the circulation in the required proportion, and act, as in the case of the adrenals, as a direct chemical stimulus.

Muscular Aids.—Abdominal respiration assists the return of blood from the splanchnic area. If an incision be made in the posterior vena cava in front of the diaphragm, then with every retreat of that muscle, pressure is exercised on the abdominal contents, and the blood spurts out of the vessel. This pressure on the contents of the abdominal cavity is one of the most important mechanical aids to the circulation. The abdominal muscles are assisted by the stout elastic fascia which plasters their external surface, the anus is tightly closed, and the pressure within the abdomen raised at each inspiration. Failure to secure this pressure results from a relaxed condition of the anus. This is frequently seen in the last stage of some debilitating diseases in the horse. The anus remains open, and allows the air to rush in and out of the bowel at every respiratory effort. In the veins of the hind-limb the whole course of the blood is directly against gravity until the posterior vena cava is reached. In that vessel gravity is in favour of the contents, for the vein falls from the spine to the heart, and the respiratory help above described completes the work as the heart is approached. The squeezing to which the liver is subjected in the abdomen is a most valuable means of assisting its circulation.

Muscular movements of the body and limbs are of the utmost importance as aids to the circulation. Muscles, by their contraction, squeeze the blood along the veins, regurgitation being prevented by the valves. Hill has shown that the column of blood in the vessels of the limbs may be broken up into segments, and by muscular action the stream to a part turned on or cut off, and the supply regulated according to its requirements. The importance of muscular action as an aid to circulation is seen every day, especially in the case of the horse. The swollen legs which are caused by standing are due to transudation, which is itself due to pooling of blood under the influence of gravity, and the absence of the venous massage which results from muscular activity. We see this condition also in the feet, where the absence of exercise means loss of the needful stimulus to the circulation in the laminæ, and the feet become congested.

It is impossible for a man in an upright position to remain absolutely immovable. The slightest change in the pressure on the limbs brings muscles into play which force the blood along the veins. The same thing occurs in the horse, an animal that may not lie down for days or weeks together (and some *never* lie down). The weight imposed upon the hind-limbs is never equally distributed during repose. First one leg, then the other, takes the weight, and at every change in posture the muscles compress the veins and force the blood along. In the fore-leg these alternate changes in position are not necessary; the veins are short and near the heart.

The experiment of holding the domestic rabbit in the vertical position referred to at p. 74 is a good example of the manner in which the blood will pool under the influence of gravity in the absence of muscular support.

It is true that in the larger quadrupeds changes of posture are of a far simpler character than in the biped, the most frequent, perhaps, being that of the head in grazing. This imposes a column of venous blood in the head and neck, from which it has to ascend against gravity. This is fully provided for by the venous cisterns beneath the masseter muscle, which at every masticatory act mechanically force the collected blood into and along the jugular, the valves preventing regurgitation. In the days of bleeding, when jugular obliteration was not uncommon, horses so affected could not be grazed, owing to the vertebral veins being unable to compensate for the posture.

The left ventricle is capable of driving the blood throughout the entire vascular system, but it needs assistance. Under the conditions of a normal circulation it drives it principally as far as the arterioles, then the skeletal muscles and valves in the veins afford the venous system the aid necessary to it, and the respiratory pump, as the heart is approached, completes the emptying of the veins and fills the right heart.

Peculiarities in the Circulation through various tissues occur as the result of their special functions. Peculiarities are observed in the brain, erectile tissues, etc. The great vascularity of the brain necessitates that the blood should pass to it with a degree of uniformity which will insure the carrying out of its functions. It must never be left without blood, or immediate unconsciousness would occur. We see this provided for by the frequent arterial anastomoses—for example, the *Circle of Willis* and the *Rete Mirabile* of ruminants, which insure that not only does the blood enter with diminished velocity, but that if a temporary obstruction occurs in one vessel its work is readily performed by the others. The rete mirabile alluded to, which forms the arterial plexus on the base of the brain of ruminants, is considered by some to regulate the flow of blood to the brain when the head is depressed during grazing, and, it is said, accounts for the absence of cerebral hæmorrhage in these animals. It is probable that this may be one of its functions, but the horse possesses no rete, and his head is depressed during grazing for more hours out of the twenty-four than is the case with ruminants. It has probably, therefore, some other function to perform.

The free anastomoses of the vessels of the brain guarantee to it an uninterrupted blood-supply. In the dog both internal carotids and both vertebrals have been ligatured without causing unconsciousness or death, the supply of blood being kept up through the anterior spinal artery. The veins of the brain empty their contents into venous sinuses which by their structures are well protected from compression. There are no valves to the openings into the sinuses, nor are there valves in the thin-walled small veins of the brain.

The circulation in the brain is peculiar, inasmuch as its substance is contained within a closed unyielding cavity. A small space formed by the membranes exists between the skull and the brain, and in this is found a little fluid, which may pass into the interior of the brain or backward into the spinal canal. The cerebral fluid acts as a water-pad, and this fluid may be rapidly absorbed, for it readily passes into the veins at any pressure higher than that in the venous circulation. Nevertheless, the space which this renders available is very small, so that the brain may be regarded as incompressible. Special provision must, therefore, exist in its circulation to guard against a rise in blood-pressure, and this is furnished by dilatation of any one set of vessels producing a constriction of the other set. By this means no increase in size nor increase in blood-capacity occurs; all that is affected is the velocity of flow. If the arterial pressure of the brain rises and that in the veins remains constant, there is an increased velocity of flow; if the arterial pressure is constant, and the venous pressure rises, there is a diminished velocity of flow.

The brain presses against the cranium with a pressure equal to the blood-pressure in the capillaries. The brain-pressure, cerebro-venous pressure, and cerebro-spinal fluid pressure have been shown by Hill to be one and the same.

If the brain be exposed it is observed to rise and fall synchronously with the respiratory movements. Expiration causes the brain to rise by hindering the return of blood, while inspiration causes it to fall by facilitating its flow. Owing to the incompressibility of the brain substance in the cranial cavity the pulse is transmitted through the brain substance to the veins, and causes the blood to issue from them in pulses synchronous with the arterial pulses.

There is no vasomotor nerve supply proved to exist in the brain.

The singular arrangement of the venous plexuses of the corpus cavernosum penis admits of this organ attaining a great increase in size, a condition which in the case of the brain every measure is adopted to prevent. The considerable size of the venous plexuses of the penis, their frequent intercommunication, the muscular pressure to which the veins leading from the sinuses are exposed, produce under the direction of the vasomotor nervous system a considerable increase in the volume of this part.

In some other organs the distribution of the bloodvessels is also peculiar. It is not known why the spermatic artery and plexus of veins should take such remarkably tortuous courses. Possibly, in some way or other, it may be concerned with the secretion of the glands, but its use is far from clear. On the other hand, tortuous vessels in the walls of hollow viscera, such as the stomach and intestines, perform a very evident function. We have only to think of the difference in size between a collapsed and of a full stomach in the horse to recognise the necessity for some arrangement existing to prevent over-stretching of the vessels or interference with the blood-supply.

The vast venous and arterial plexuses of the foot of the horse are a peculiarity in the circulation dealt with in the chapter devoted to the Foot.

Pathological.

A man is considered to be as old as his arteries, but a horse may be stated to be as old as his feet and legs.

It is a remarkable fact that very little of the strain of the hard life of a horse falls on his arteries; with age the vessels become more rigid, but no sudden strain produces aneurisms, such as might be expected from the class of work performed; this is probably due to the fact that he does not suffer from syphilis. There is, however, one kind of strain which arises in the hunting field, or under similar circumstances, in which the walls of the external and internal iliac arteries suffer; in consequence of this a **thrombus** forms in the vessels, which become partly or completely obliterated. Collateral circulation suffices in a state of repose, during which not a sign of any circulatory trouble is evident, but as soon as the animal gets to work sudden and painful muscular cramps occur, and finally temporary paralysis follows. These symptoms, accompanied by intolerable pain, completely pass away with rest and return with work.

Parasitic trouble of the vessels is very common, the main seat being the anterior mesenteric artery, which is rendered rigid and aneurismal, and has its lumen obliterated by *Strongylus armatus*. It is remarkable how very little interference with the intestinal circulation occurs in consequence of this parasitic invasion, and it is equally astonishing how few horses are free from this infection. It is probably the most widely spread equine parasite.

Pulse.—The older physicians studied the pulse with care; at the present day it does not receive the same amount of attention. It is not sufficient to know the number of pulsations; the important thing is the *character* of the wave.

A pulse may be *quick* or *slow*. Either of these may be *strong*, *weak*, *hard*, or *soft*. Strong and weak refer to the force of the ventricular contraction; hard and soft refer to the tension as judged by the finger—viz., the amount of pressure required to obliterate the pulsations. A further division of pulses is into *large* and *small;* this group refers to the volume of the artery. There is no pulse specially indicative of any given affection, but the *character* of the pulse in the prognosis of disease is of the utmost clinical value.

CHAPTER IV

RESPIRATION

SECTION 1.

The Lungs.

The Chest Wall.—The chest is formed of the moderately rigid case furnished by the ribs and the flexible wall provided by the diaphragm. The contents of the chest are vascular and respiratory, and the provision made for their protection is not quite the same in each case. The vascular contents are situated mainly in the anterior portion, for here the heart is found with its blood-vessels, while relatively speaking there is only a small amount of lung. The horizontal spine of all animals requires the ribs to perform a function not required in the biped. It would exceed the space at our disposal to deal with the peculiarities of the chest wall in all animals. That of the horse may be selected as a type, more particularly on account of its practical importance.

It is usual to speak of the ribs as true and false, but this tells us nothing as to their function. The true or sternal ribs form a case for the vascular organs, and help to support the horizontal spine. To enable them to do this they are shorter, stouter, and straighter than the false, or, as we would prefer to call them, respiratory ribs. Further, they are all inserted into the sternum either directly, as the first pair, or indirectly by means of cartilage, as the remaining seven pairs. The chest is very narrow between the two first ribs, but rapidly increases in width, as may be seen in the following measurements, taken at the widest place between each pair of ribs in a riding-horse of medium height:

	Mm.	Inches.	Increase from Rib to Rib. Inches.
1st pair of ribs: greatest distance apart	90	3½	0
2nd ,, ,, ,, ,, -	115	4½	1
3rd ,, ,, ,, ,, -	160	6¼	1¾
4th ,, ,, ,, ,, -	191	7½	1¼
5th ,, ,, ,, ,, -	230	9	1½
6th ,, ,, ,, ,, -	280	11	2
7th ,, ,, ,, ,, -	355	14	3
8th ,, ,, ,, ,, -	420	16½	1½
9th ,, ,, ,, ,, -	470	18½	2

This table shows how rapidly the chest increases in width from front to rear, and the rate of that increase from rib to rib. If a vertical section of the chest be made, say between the fifth and sixth ribs, the thoracic cavity will be found egg-shaped, the broad part being above, the wall curving inward to obtain a hold in the sternum. From the first to the sixth rib the main function of the chest wall is to form a case for the vascular apparatus and to support the horizontal spine. The lateral movemnts of the sternal ribs are of no importance from a respiratory point of view. Some, like the first pair (Fig. 40), have no lateral movement, and it is very limited in the others, though it increases farther back in the chest. Under forced respiration the fifth rib may take a limited share in respiration, but practically none of those anterior to it have any movement.

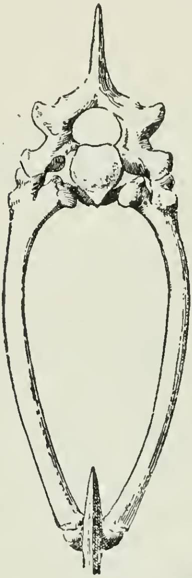

Fig. 40.—First Pair of Ribs in the Horse (after Schmaltz: *Atlas d. Anat. d. Pferdes*).

Note the way in which the head and tubercle are disposed in order to prop up the spine.

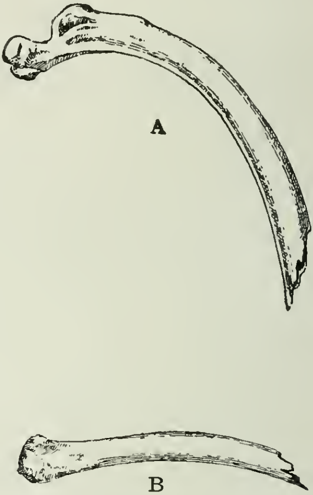

Fig. 41.—Head of the Eighth and Sixteenth Rib of the Horse (after Schmaltz: *Atlas d. Anat. d. Pferdes*).

A is the eighth rib in normal position; the tubercle is still above the head. B is the sixteenth rib in position; the tubercle now lies behind the head, and cannot be seen from the front.

The relatively rigid cage formed by the first to the sixth ribs articulates with the spine, and it might be supposed that some rib movement favourable to respiration must occur, or the ribs would not form a joint with the spine; but this series of joints is of far more importance in securing flexibility of the spine than in respiratory functions, while the manner in which they articulate shows that they are propping the spine up—a feature which is in marked contrast to the false ribs. If the true ribs be examined, it will be found that both the head and tubercle are large and well developed, the tubercle being disposed above the head (Fig. 41, A), and both so arranged towards the vertebræ that they prop it up. From the first to the seventh rib the substance and strength of rib is very evident; from the eighth backwards the ribs decrease in size, both in width and depth, and the decrease in substance becomes progressively greater. From the first to the thirteenth rib the tubercle is above the head, but from the fourteenth backwards the tubercle is placed lower and lower, and finally is in the same horizontal plane as the head (Fig. 41, B). The tubercle begins to descend from the point where the ribs are so far removed from the sternum that no further propping up of the spine is possible.

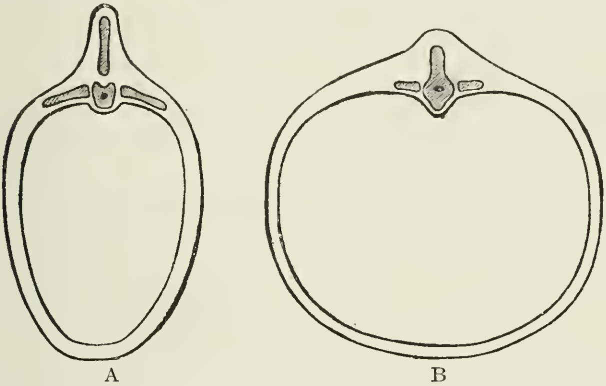

FIG. 42.—VERTICAL SECTION OF THE BODY THROUGH THE EIGHTH AND SEVENTEENTH DORSAL VERTEBRÆ.

A, Eighth dorsal; B, seventeenth dorsal section.

The anterior part of the thorax is narrow in order to accommodate the fore-legs, which are, as it were, plastered on to it.

The false ribs have no sternal insertion, but each is connected with the one in front by means of a piece of cartilage; while rigidity of the walls is characteristic of the anterior chest, mobility is characteristic of that portion now being considered. The false ribs are narrow, thin, and curved. The curve gives the barrel shape to the side of the chest. Further, these ribs before they curve downwards have a relatively level or flat surface on their upper part, and on this the actual width of the back depends. From the ninth to the eighteenth the ribs decrease in length. The respiratory portion of the thorax extends from the seventh to the eighteenth rib. The movement of the ribs is mainly of two kinds. At their upper part they are partly everted and pulled forwards, below they are thrust outwards. The curvature of the rib is of value when the process of eversion is attempted, for by means of this curvature very little eversion represents a distinct increase in the transverse diameter of the chest cavity. The semicircle formed by the cage is well seen in vertical section in Fig. 42, A and B, made at the anterior and posterior part of the thorax.

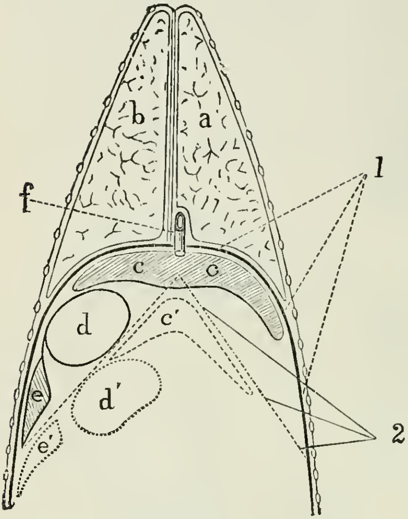

FIG. 43.—HORIZONTAL SECTION OF THE HORSE'S CHEST LOOKED AT FROM ABOVE (SUSSDORF-ELLENBERGER).

a, Right lung; *b*, left lung; 1, position of the diaphragm during deep expiration; *c*, liver during deep expiration; *d*, stomach during deep expiration; *e*, spleen during deep expiration; 2, position of diaphragm during deep inspiration; *c′*, position of liver; *d′*, of stomach; *e′*, of spleen during deep inspiration; *f*, posterior vena cava as it passes through the diaphragm.

A front to rear section of the chest (Fig. 43) is roughly egg-shaped, the narrow end of the egg in front, while the broad end is cut off obliquely for a considerable distance by the diaphragm. Of the latter we shall speak in detail presently, but it may be noted that the movements of the diaphragm and the other muscles of inspiration are capable, during quiet respiration, of lengthening the front to rear diameter of the chest by 10 to 12 cm. (4 to 5 inches), while at the widest part of the chest wall, viz., between the eleventh and twelfth ribs, the increase in side to side diameter is about 4 cm. ($1\frac{1}{2}$ inches).

Movements of the Diaphragm.—The vast musculo-tendinous sheet placed between the abdominal and thoracic cavities merits detailed consideration, owing to its importance in the respiratory mechanism. This muscle is placed obliquely forward in the body, and extends from the region of the loins to the sternum. It roughly corresponds to the borders of the false ribs on both sides. In the right of its centre it is penetrated by the posterior vena cava; to the left and above its centre it is perforated to receive the œsophagus. Hung on to it are the liver wholly, and the stomach partly, and if it were not for two powerful tendons and muscles let into it from above, known as the cruræ, these weights could not be supported. Between the branches of the cruræ the posterior aorta escapes from the chest. The tendon of the diaphragm is centrally placed, and forms a dense feltwork of fibres, while the circumferential portion of the organ is muscular. The diaphragm is convex towards the thorax, resembling an open umbrella. This convexity is due to the pull exerted on it by the diminished pressure in the air-tight thorax, supplemented by the pressure of the abdominal viscera from behind. The diaphragm maintains its dome shape towards the thorax so long as the chest is air-tight. Even under pathological conditions, when the muscle is burdened by the effusion of gallons of fluid poured into the chest, no flattening of the diaphragm occurs.

The cavity of the chest is not cut off cleanly and sharply by the diaphragm. The central part of the latter is thrust forward into the chest, and by its projection separates the two lungs at their posterior part, which in consequence rest on or wrap themselves around the diaphragm, and as it were envelop it. The lungs, when fully distended, do not reach within 8 cm. (3 inches) of the cartilages of the false ribs. These points may be seen in Fig. 44, which gives a side view of the horse's chest. AFE indicates the margin around which the diaphragm is attached; the dotted line suggests the central part of the diaphragm thrust forward into the cavity of the chest on either side. This is covered by the lungs to within a short distance of the false ribs. If, therefore, the chest were punctured transversely anywhere below the dotted line in the diagram, and the instrument pressed through to the opposite side, the structures would suffer in the following order: lung, diaphragm, abdominal cavity, diaphragm, lung. To state these facts briefly, the largest respiratory area of the lungs lies on an obliquely placed dome-shaped table formed by the diaphragm, which projects into the chest.

The diaphragm recedes on inspiration, being pushed back into the abdomen, but the retreat does not occur evenly over its whole area. The central part of the diaphragm is naturally restrained by the posterior vena cava, the upper part and ribs move freely, while in the lower half—viz., from the vena cava to the sternum—the movement is again somewhat restricted. As the diaphragm recedes it compresses and carries back the whole of the abdominal viscera, more especially the liver, stomach, and spleen. The diaphragmatic curve of the colon is also carried back to a limited extent. But the chief result arising from the backward movement of the diaphragm is that on the circulatory system. Blood-pressure in the posterior vena cava is increased, the phrenic veins are emptied, and the portal vein is filled. The to-and-fro action of the muscle is a most important aid to the circulation. The limitation in movement of the central portion of the diaphragm suggests that no flattening of it occurs during inspiration, and this view is supported by X-ray inspection in smaller animals. The viscera behind the diaphragm are affected by each of its backward and forward movements (see Fig. 43). The abdominal contents bulge forward, as it were, into the chest, and so behave, to quote Keith's apt description, like a piston being driven to and fro (see Fig. 45).

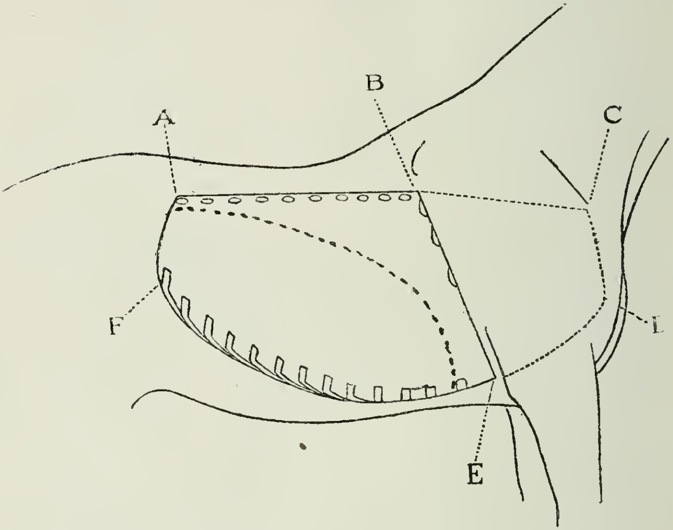

Fig. 44.—Diagram of the Extent of the Chest in the Horse and Position of the Diaphragm.

The area B, C, D, E, is under the scapula and its muscles, and practically not available for auscultation; the surface A, B, E, F, is the available area of the chest wall. The lung reaches to within a hand's breadth of the false ribs. A, F represents the last rib; B, E runs parallel to the posterior edge of the triceps; C, D corresponds to the position of the first rib.

The diaphragm bulges into the chest centrally, thus separating the two lungs. The curved dotted line falling from A to E represents the central line of the diaphragm, and shows the extent to which it encroaches on the chest.

The lungs contain more air during a deep than during an ordinary inspiration, so that the chest cavity is automatically reduced in size during an ordinary inspiratory effort because of the reduction in the amount of lung inflated. Fig. 46, slightly modified, from Ellenberger and Baum, shows the position of the lungs during normal inspiration.* The lungs are resting on the diaphragm, and it will be observed that this muscle may be seen passing to the ribs for attachment. During ordinary inspiration the portion of the thoracic cavity not occupied by the lungs is temporarily obliterated by the abdominal viscera being thrust forward, and thus pressing the diaphragm against the ribs and so closing the potential space. In Fig. 46, if the lungs were fully distended during the forced inspiration of work, they would extend to where the diaphragm is attached to the ribs—viz., about 4 inches above the edge of the cartilages of the false ribs. In Fig. 44, A, the dotted line under the loin indicates the limiting position of the lungs during a forced inspiration. During the ordinary inspiration of repose the dotted line would end farther forward.

The pressure behind the diaphragm can be realised by an inspection of Ellenberger's figures (Figs. 45 and 46). When this pressure against the diaphragm, especially during fast or heavy work, is considered, there is no difficulty in understanding why this muscle so frequently ruptures in the horse, and, as we shall see later on, this same cause, pressure, may help to explain the far more common lesion of ruptured stomach. Ellenberger represents the lungs as occupying a relatively very small portion of the thoracic cavity during expiration. His figure is not reproduced, as we think the representation of the collapsed lung is likely to prove misleading.

Briefly, the chest cavity of the horse is so arranged that it accommodates itself to the needs of respiration; during repose a large portion of it can be completely blotted out by the muscular rim of the diaphragm adhering to the pleura. During work this potential space, indicated at 3, 3 (Fig. 46), is filled by the now greatly enlarged lungs.

The Lungs Fill with Air.—Air is never completely absent from the healthy lungs, even after death. On life ceasing they retract, especially from the diaphragmatic region, and shrink upwards towards the spine. If they be now distended artificially, the organs gradually fill, those portions nearest the bronchus distending first. There is no sudden or unusual swelling, but rather a gradual invasion of different but neighbouring areas, which gradually come nearer and nearer together, and finally meet. The parts to expand last are the edges of the lungs and the surface in contact with the diaphragm, especially with its upper half. It is not intended to infer from these post-mortem observations that the distension of the lungs during life is identical, because during life they are never collapsed to the same degree, and

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* The writer's view is that the lung is not shown sufficiently distended.

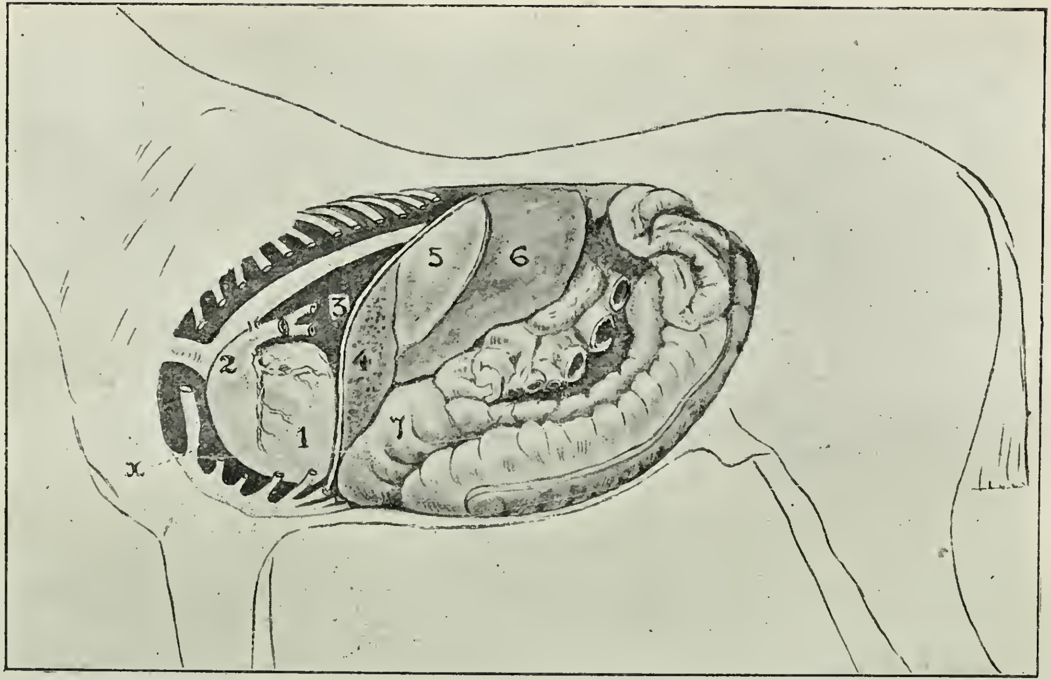

FIG. 45.—POSITION OF THE ABDOMINAL VISCERA AND DIAPHRAGM AT THE END OF EXPIRATION (AFTER ELLENBERGER AND BAUM: *Topographische Anatomie des Pferdes*).

1, The left ventricle; 2, pulmonary artery; 3, pulmonary veins; *x*, second rib. Note the oblique position of the heart in the chest, with its right ventricle inclining towards the sternum; also the suspension of the heart by means of its vessels. The encroachment of the central part of the diaphragm is well seen. 4 is the cut surface of the liver; 5, part of the greater curvature of the stomach; 6, the spleen; 7, the large colon. The pressure against the diaphragm is very obvious

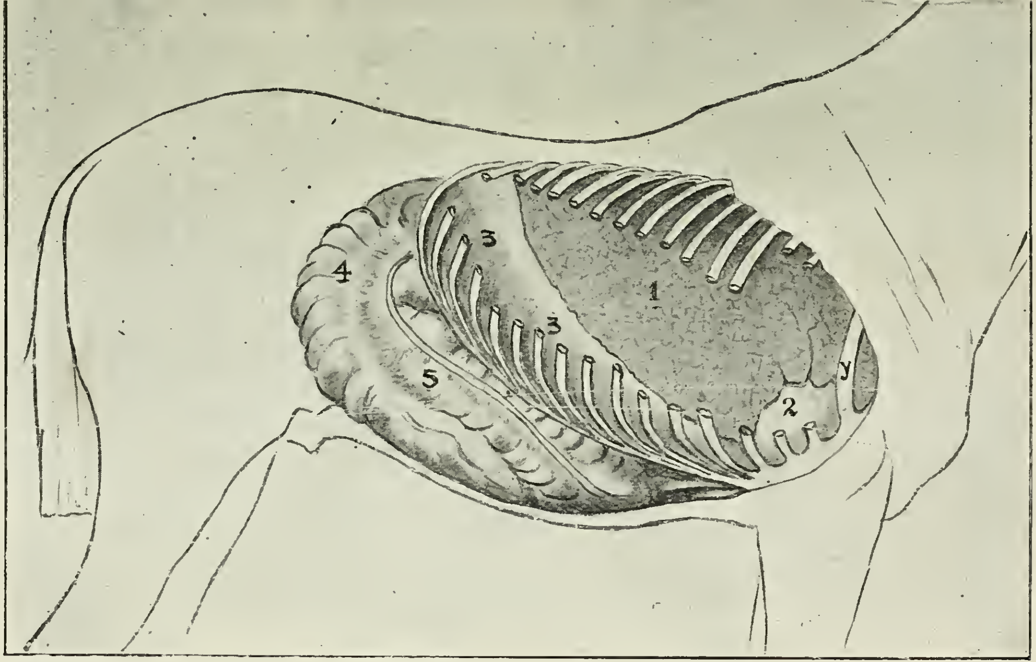

Fig. 46.—The Lungs, Diaphragm, and Abdominal Viscera in Position during Quiet Inspiration (after Ellenberger and Baum: *Topographische Anatomie des Pferdes*).

1, Right lung; 2, the heart; 3, the diaphragm; 4, the large intestines; *y*, second rib.

These drawings were made from frozen sections. We do not regard the lung as sufficiently distended even for a quiet inspiration.

further, when distended after death, they inflate in the line of least resistance. Nevertheless, all parts of the lung are not equally distensible. The part situated around the roots of the lungs must necessarily, from the obstruction offered by the bronchi, be less distensible than those parts farther removed. The anterior lobes, in consequence of the rigid nature of this part of the thoracic cage, can hardly move at all, though, of course, they are kept distended. The greatest amount of expansion occurs where there is the greatest amount of spongy lung-tissue and the least amount of bronchial ramification, and this necessarily exists in the outer zone of the lungs, particularly towards that portion facing the diaphragm, and corresponding to that part of the chest where the greatest movement occurs.

From this it must not be inferred that the lung in other places does not expand. As a matter of fact, the lungs fill up in the living animal every crevice not occupied by heart or vessel. There is no such thing as a pleural cavity in the healthy chest. The lungs lie close against the ribs, and never leave ribs or diaphragm during the whole life of the animal so long as health exists. There is, of course, a space between the costal and pulmonary pleura, but in health it is only a potential space, and there is a second potential space during repose, as already described, between the muscular rim of the diaphragm and the margins of the ribs. A finger introduced into the chest finds the lung close up against the opening which has been made, and if an attempt be made to inject fluid into the potential pleural sacs, the close application of the lung against the chest wall prevents it as effectually as it prevents a piece of soft rubber tubing from being passed along between the costal and pulmonary surfaces. The lung exposed by this small opening may even bulge outwards under the pressure of the inspiratory act.

These facts must not be confused with those which may be observed under pathological conditions, when, the lungs having collapsed under hydrostatic pressure, as in the case of effusion into the chest, air readily enters the cavity through the cannula when the level of the fluid is lowered by tapping; for the lung is no longer in contact with the chest wall, having collapsed upwards towards the spine.

The areas affected in pneumonia might indicate which are the essential and which the non-essential portions of the lung in ordinary respiration. Pneumonia always affects the lower lobes of the lung, and nearly always the anterior lobes as well. The latter, owing to the curve of the spine, are on a lower plane than the upper lobes. It might be supposed from this that the upper part of the lung was of more respiratory importance than the lower, for with this surface of lung left the pneumonic patient can live for days. But in the upright animal the lower part of the lung is also the first in which pneumonia appears, and the lower part in the biped is the extreme upper part in the quadruped, from which it would appear that it is not necessarily the least efficient portion of the lungs in which pneumonia begins, though doubtless in the horse the least useful portion of both lungs is the anterior lobes.

Though we have attempted to indicate that some parts of the lung are of more use than others, and that these parts are mainly filled during ordinary respiration, it must not be inferred either that the remaining portions are quiescent or that the lungs are firmly anchored within the chest. As a matter of fact, the roots of the lungs are carried back with each inspiration, and come forward at each expiration, and it is this which explains the up-and-down tracheal movement of the horse in hurried respiration.

A small hole into the pleural sac of the horse does not lead to collapse of the lungs, but a large opening does. Even then the lungs continue partly to distend and recoil, but only with difficulty, and finally asphyxia occurs. In all animals in which no communication between the pleural sacs exists, the collapse of the one lung under the influence of a large opening into the chest is followed by the opposite lung doing extra work, and even bulging across the middle line of the chest in the mediastinal region.

In dealing with the distension of the lungs, the condition of repose has been assumed. If work be done, the respirations are increased. They are shorter and shallower, and may vary from 20 to 100 or more per minute, depending upon the nature of the work and the fitness of the animal. In such cases the lungs remain more fully distended than during repose, but the actual amount of air entering at each inspiration is less, owing to the fact that the respirations are more numerous, the rule being that when the rate of breathing is increased the depth is decreased.

Inspiration.—We have seen that during life the lungs occupy the cavity of a rigidly air-tight chest. So long as this air-tight condition is maintained, any movement which tends to increase the size of the chest causes distension of the lungs. By distension expanding, the air within them becomes rarefied, and thus a difference in pressure occurs between the outside air and that already in the lungs. In consequence, air rushes in to restore equilibrium, and this inrush is inspiration.

An increase in the size of the chest in its two diameters is caused by the movements of the diaphragm and the false ribs. The former retreats and carries with it the abdominal viscera, which are in consequence exposed to compression squeezed together. The ribs generally are pushed outwards, while above they are drawn forwards, and their posterior edge everted, by which means the natural curve of the rib increases the side-to-side diameter. At the same time the intercostal spaces widen. By these means the capacity of the chest is increased, and the lungs at once fill the space thus created.

The tendency of the lungs is to recoil, owing to the highly elastic nature of their tissues, and the fact that they are normally in a state of distension. In the post-mortem condition they are much smaller than the chest. During life the chest cavity, being air-tight and larger than the lungs, the latter are distended by the atmospheric pressure within them.

During forced inspiratory movements the elbows are turned out, which brings auxiliary muscles into play, and allows a certain number of true ribs to take part in the chest movement.

Expiration.—The chest having been filled with air, the next process is its expulsion, and physiologists are not entirely agreed upon the mechanism at work here. At one time expiration was considered to be a purely non-muscular act, the elastic recoil of the lungs and of the abdominal muscles being the important factors; but if the forward movement of the abdominal contents is to be credited with any influence in expiration, it is evident that the action of the abdominal muscles cannot be of the nature of an elastic recoil. There is some experimental evidence suggesting that a reflex nervous co-ordination exists between the inspiratory and the abdominal muscles, so that, as the former cease to act, the antagonists at once come into operation. It will be shown later that this holds true of the muscles of locomotion, and there seems no reason why it should not apply to the muscles of inspiration and expiration. At any rate, the fact is undoubted that the contents of the abdomen travel chestward, and there seems no great reason why this should be brought about by the elastic recoil of the lung, and of the abdominal muscle, when a purposive movement, for which every facility exists, would be more to the point. As the abdominal contents are forced backwards in inspiration, the gaseous contents of the intestine are submitted to compression. This may be turned to useful advantage during the period of recoil. There is also the elastic recoil of the cartilages of the false ribs, seeking to return to their position of rest after inspiration; but as material contributions to the effort of expiration, the two elastic recoils are not of any great value.

Expiration is considered by some physiologists as a passive act, and this view is partly based on the fact that it still continues after all nervous supply to the muscles is cut off. If the cord be divided below the origin of the phrenic nerves, all the muscles of the body posterior to that section are paralysed, but expiration still continues, owing to the elastic recoil of the lungs.

Costal and Abdominal Respiration.—In the human subject two types of respiration have been described, one costal, as in a woman, and one abdominal, as in a man. It is now generally admitted that the costal type in the woman is an artificial condition, the result of compression. In the lower animals the breathing is essentially abdominal.

The **Fœtal Lung** contains no air, and therefore sinks in water. The first few inspiratory gasps at birth distend the alveoli, but for some time the conditions present in the adult, viz., the negative pressure in the pleural cavity, and the collapse of the lungs on opening the chest, are not found in the very young animal. They occur only when the cavity of the thorax is larger than the lung in a state of collapse. In the fœtus the lungs exactly fill the chest in the condition of expiration, and it is not until the chest cavity grows, as it were, too large for the lungs that a negative pressure in the thorax is produced. Later on (p. 142) the cause of the first act of breathing will be explained. Thoracic development in young animals is very rapid; a foal will increase 4 cm. (1½ inches) in circumference within the first few hours after birth; when this absolute increase in chest capacity is established, a negative pressure in the pleural cavity is obtained.

Muscles of Respiration.—The action of the muscles of the chest during respiration has been much disputed. The external intercostals doubtless, from the direction taken by their fibres, pull the ribs forward, and by so doing increase the transverse diameter of the chest; in this respect they are regarded as inspiratory muscles. The internal intercostals, the fibres of which run in an opposite direction to those of the external, draw the ribs backwards and act as muscles of expiration; and speaking generally, we may say that those muscles which draw the ribs forward are inspiratory, whilst those which draw them back are expiratory. The following table shows the inspiratory and expiratory muscles of the chest:

Muscles of Inspiration.	*Muscles of Expiration.*
Diaphragm.	Abdominal muscles.
External intercostals.	Internal intercostals.
Serratus anticus.	Transversalis costarum.
Levatores costarum.	Serratus posticus.
Serratus magnus (during laboured respiration).	Triangularis sterni.
Latissimus dorsi (during laboured respiration).	
Scaleni (during laboured respiration).	

In most quadrupeds the sternum is fixed to the ribs and undergoes little or no movement; even the most powerful respiratory movements in the horse give rise to no sternal movement. On the other hand, there is a moderate amount of movement between the last two or three sternal ribs and their cartilages, and a good deal of movement between the false ribs. During laboured respiration any muscle which can assist in advancing the ribs directly or indirectly is brought into play. This is well marked in dyspnœa.

After the expiratory act there is a pause before the next inspiration. In the horse at rest the period of expiration is as a rule longer than that of inspiration, though the proportion between the two is not invariable. During work the duration of the inspiratory and expiratory acts is about equal.

Intrapulmonic and Intrathoracic Pressure.—During inspiration a slight negative pressure exists in the trachea, and during expiration a slight positive pressure. A strong inspiration, with the glottis closed, such as can be made by a voluntary effort in man, rarefies the air in the respiratory passage and the pressure falls. Conversely a strong expiratory effort, with the glottis closed, as in coughing, defæcation, or parturition, raises the pressure in the respiratory passages considerably, and thereby increases the intrathoracic pressure. The increased pressure within the respiratory passages and thorax influences blood-pressure, for the veins leading to the heart are partly obstructed, as may be witnessed, for example, in man in a violent fit of coughing, and thereby the venous flow to the heart is lessened. In the pleural cavity a negative pressure is always present, due to the tendency of the elastic lungs to collapse. The value of this pull of the lungs on the chest wall has been ascertained for the sheep to be about 3 mm. ($\frac{1}{8}$ inch) of mercury, and during dyspnœa 9 mm. ($\frac{3}{8}$ inch). In the dog during inspiration the negative pressure in the pleural sac is 6 mm. ($\frac{1}{4}$ inch) of mercury; whilst during expiration 3 mm. ($\frac{1}{8}$ inch) has been observed. In the horse 6 mm. ($\frac{1}{4}$ inch) has been registered during a powerful expiration, and 28 mm. ($1\frac{1}{8}$ inches) during a powerful inspiration. The negative pressure can be recognised post mortem by the rush of air immediately the chest is punctured.

When the chest is opened during life, the atmospheric pressure within and without the lungs is equal, and in consequence the lungs shrink and in time collapse. In the horse a large wound of the chest cavity is serious, for the reason that the two pleural sacs communicate, and therefore both lungs shrink and finally collapse. The collapse is gradual and leads to death by asphyxia. unless the chest wound can be perfectly sealed, in which case the air in the chest cavity is absorbed, and the negative thoracic pressure restored. On the other hand, a small penetrating wound of the chest does not cause collapse of the lung, for the organ distends and pneumatically closes the pleural space.

The **Number of Respirations** varies with the class of animal; as a rule, the larger the animal the slower the respirations.

Horse	8 to 10 per minute.
Ox	12 ,, 15 ,, ,,
Sheep and goat	12 ,, 20 ,, ,,
Dog	15 ,, 20 ,, ,,
Pig	10 ,, 15 ,, ,,

Rumination increases the frequency of, and causes irregularity in, the respiration, and in all animals muscular exertion at once causes it to rise. In experiments on respiration this is most marked; walking a horse will nearly treble the number of respirations, but the rate of breathing begins to fall immediately the horse stops, though it does not reach the normal for a few minutes.

The ratio of heart-beats to respiration has been placed at 4 : 1 or 5 : 1.

The Effect of Respiration on the Circulation.—We have previously alluded to the influence of respiration on the circulation, and have pointed out that the negative pressure in the thorax assists the circulation by favouring the return of blood by the veins. This aspiratory action of the thorax mainly affects the anterior vena cava, but the contents of the posterior vena cava, we have seen, are also influenced during inspiration by the contraction of the diaphragm and the consequent compression to which the vessels are subjected. These two important features of the respiratory system have the effect of increasing at each inspiration the flow and velocity of the blood to the heart. Aspiration of the thorax favours the filling of the right heart, while the distension of the lungs in inspiration is generally believed to dilate the vessels, and so favour the flow of blood through these organs.

In dealing with the question of blood-pressure (p. 74), it was pointed out that the curves obtained show certain undulations which are generally regarded as due to the influences of respiration, for it is found, if the blood-pressure and respiration curves be simultaneously obtained and superposed, that the undulations in the latter correspond very closely to the undulations in the blood-pressure curve. On comparing the curves, it is found that the blood-pressure rises with inspiration and falls with expiration; further, it is observed that the rise does not take place immediately inspiration begins, nor does the fall occur immediately expiration starts, but shortly after in both cases, as may be seen in Fig. 29. These results have never been adequately accounted for; until the question was reopened by Lewis in recent years, the following was the explanation given of the respiratory rise and fall of blood-pressure:

If the curves be closely examined, it will be found that during inspiration the pulse frequency is increased, while during expiration it is decreased. This increase appears to hold good for all animals, and is considered to be due to a diminished activity of the cardio-inhibitory mechanism, while the reduction in pulse-rate is believed to be caused by a stimulation of the same centre. Any increase in the action of the heart results in more blood being thrown into the aorta, and so raises the blood-pressure, which is further raised by the aspiratory action of the right auricle in sucking in blood from the veins. So far, then, the general causes of a rise in blood-pressure during inspiration can be explained. The next thing to account for is the delay in the rise at the beginning of inspiration, and this is considered to be due to the dilatation of the lungs causing an increase in the capacity of the pulmonary vessels. The result of the increase is that they have to be filled, and the delay thus caused explains the delay in the rise of blood-pressure. In expiration the pulmonary vessels become smaller, and the delayed fall in pressure is attributable to these vessels having not yet returned to their expiratory capacity.

Such, then, was the explanation accepted by most physiologists, but in recent years the investigation of the phenomena by T. Lewis has resulted in considerable light being thrown on the matter. This observer shows that the respiratory curves of blood-pressure are of very complex origin, and unless the character of the respiratory act be known, it is not possible to say what the effect on the blood-pressure will be. In a man trained to breathe with his ribs, the blood-pressure falls during inspiration and rises during expiration; when abdominal breathing is practised, there is a rise during inspiration and a fall during expiration; and with costal and abdominal respiration combined, intermediate results are obtained.

The secondary inspiratory rise of blood-pressure which follows the fall, where respiration is slow and the costal type of breathing is present, is, according to Lewis, due to lessened intrapleural pressure, which causes lessened pressure on the heart, and in consequence an increased filling of the organ. He was able to show, by introducing or withdrawing air from the pericardial cavity, how sensitive the heart is to an increase or reduction of intrapericardial, and therefore of intrapleural, pressure.

The Nostrils.—Before the air reaches the lungs it is warmed by passing through the nasal cavities, so that it enters the trachea at nearly the body temperature. The incoming air also becomes saturated with water vapour, this saturation likewise occurring in the nasal chambers. In the majority of animals air may pass through either the nose or mouth to enter the trachea, but in the horse, owing to the length of the soft palate, nasal respiration alone is possible; in this animal we therefore find the nasal chambers with their inlets and outlets well developed. The opening into the nostrils of the horse is large, funnel-shaped, and capable of considerable dilatation; it is partly cartilaginous and partly muscular. Immediately inside the nostril is a large blind sac, termed the **false nostril**, and one of its uses appears to be to increase the capacity of the nasal opening by allowing considerable and rapid dilatation. Another use is the production of the peculiar snorting sound made by a horse either when he is alarmed or very 'fresh.'

During forced inspiration the nostril expands, especially the outer segment—viz., that part in communication with the false nostril—and the air is rapidly drawn up through the nasal chambers; during expiration the outer segment of the nostril collapses, but the inner segment, composed principally of the cartilaginous ala, dilates. Thus the movement of the outer and upper part of the nostril is principally inspiratory, of the lower and inner part mainly expiratory, producing a peculiar double motion of the nostrils, well seen after a gallop or in acute pneumonia (Fig. 47). The dilatation of the inner segment of the nostril is brought about by muscular contraction and by the rush of expired air; striking the cartilaginous wing of the nostril, the current is directed outwards at an obtuse angle to its course down the nostrils, as may be well seen on a frosty morning when a horse is respiring rapidly.

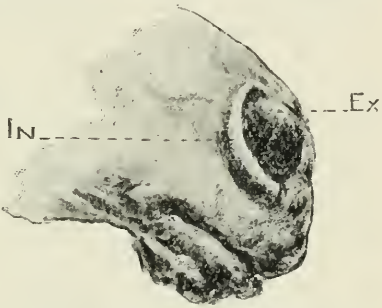

FIG. 47.—NOSTRIL OF HORSE.
In, The inspiratory portion; *Ex*, the expiratory portion.

The nasal chambers are remarkable for their great depth and narrowness; the cavities are partly filled by the turbinated bones, which nearly touch the septum on each side, so that a deep but thin column of air passes through the chambers; this arrangement insures that the air is saturated with vapour and raised to the proper temperature. The nasal chamber is divided into two parts, the lower or respiratory and the upper or olfactory. The latter will be dealt with under the Senses. It comprises the upper portion of the superior turbinated bone, the ethmoid cells, and a portion of the middle meatus; the respiratory channel, on the other hand, lies in the inferior part of the nasal chamber, and comprises the inferior meatus, inferior turbinated bone, part of the superior, and part of the middle meatus. The superior meatus may be said to exist for the purpose of smell, the inferior for respiration, while the middle connects the sinuses of the face with the nasal passages.

The termination of the two turbinated bones and their connection with the external nostril is not as a rule fully described in anatomical works. The soft, fleshy appendix of the superior turbinated bone, having divided and then reunited, is inserted into the cartilage of the nostril. In Fig. 47 the portion of the nostril marked *Ex* would have to be lifted upwards and outwards to show the seat of insertion of this bone. The lower turbinated bone also terminates in a fleshy appendix much larger than that of its neighbour. It divides: one branch is inserted into that portion of the nostril indicated *Ex* in Fig. 47, close, but external to, the appendix of the upper bone; while the inferior division is inserted into the floor of the nostril. In order to show its insertion, the portion of the nostril *In* (Fig. 47) would have to be pulled outwards. The opening into the nasal chambers is formed, therefore, by the two fleshy terminations of the inferior turbinated bone, and in forced respiration these two divisions separate widely.

The Glottis.—The air having been warmed by passing over the septum and turbinated bones, enters the glottis, the arytenoid cartilages being separated to a greater or less extent to enlarge the opening. In quiet respiration this enlargement of the glottis is not very marked, but during work the cartilages are drawn powerfully upwards and backwards, and the **V**-shaped glottis fully opened (Figs. 54 and 56, pp. 149, 151). It is a remarkable fact that the laryngeal opening should be relatively so small, considering the diameter of the trachea and the size of the nasal openings.

During inspiration the larynx and trachea descend slightly, while they ascend during expiration. This is particularly well seen in horses during the hurried respirations of disease, producing as it does a well-marked rhythmical movement of the laryngeal region and base of the tongue.

The Facial Sinuses are cavities in the face communicating with the nasal chambers; they are of considerable size, occupying nearly the entire facial region, and they give the needful bulk to the head without adding to its weight; they are lined by a membrane which is continuous with that of the nose. These sinuses are filled with air which enters them through a foramen at the posterior part of the middle meatus; during every act of respiration air is passing into or out of them. At first sight it would appear that air ought to enter the sinuses during inspiration, but the reverse is the case; it is only during expiration that they are filled, whilst during inspiration air is sucked out. Considering the position of the common inlet to these sinuses, it is difficult to understand why they should fill during expiration, though the advantage of hot instead of cold air entering is evident.

Respiratory Changes in the Air and Blood.—The changes which air undergoes on passing into the lungs must now be considered.

ATMOSPHERIC AIR CONTAINS IN 100 PARTS AT 0° C. AND 760 MM. (30 INCHES)—

	By Volume.
Oxygen	20·96
Nitrogen	78·09
Carbon dioxide	00·03
Argon	00·94
Helium	Traces
Hydrogen	Traces

The proportion of carbon dioxide is small; it is a natural impurity in the air, though essential to plant life. The atmosphere also contains moisture, the amount of which depends upon the temperature; the higher the temperature the greater the amount of water which the air can contain as vapour, and the lower the temperature the less the amount. Air may be dry or saturated, the latter term implying that it contains as much vapour as it can hold at the observed temperature; it generally contains about 1 per cent. of moisture, and is spoken of as dry if it contains ¼ per cent. The air which passes from the lungs is always saturated with moisture.

When air is taken into the lungs it alters in composition: it loses a proportion of its oxygen and gains in carbon dioxide, as may be seen in the following table:

	Nitrogen.	Oxygen.	Carbon Dioxide.
Composition of inspired air	78·09	20·96	0·03
” ” expired air	78·09	16·02	4·38
		−4·94	+4·35

The volume of oxygen absorbed is slightly greater than that of the carbon dioxide which takes its place, so that if dried and reduced to standard barometric pressure and temperature, the volume of *dry* air expired is slightly less than that of the air inspired. But since expired air is usually warmer than inspired,* and is saturated with aqueous vapour, the volume expired is actually greater.

Respiratory Quotient.—The proportion which the volume of oxygen absorbed bears to the volume of oxygen returned as carbon dioxide is termed the **Respiratory Quotient.** It shows the proportion of oxygen required to oxidise carbon, and is expressed as $\frac{CO_2 \text{ given off.}}{O_2 \text{ absorbed.}}$ The quotient on a *carbohydrate diet,* such as starch, is high, though rarely greater than 1, and generally about 0·9; for in starch the oxygen and hydrogen of the molecule exist in the proportion to form water, so that only the carbon remains to be oxidised. The quotient may, as has been said, be unity, or nearly so, depending upon whether the whole, or nearly the whole, of the O_2 is returned as CO_2. If a purely carbohydrate diet could support life, the R.Q. would be 1 exactly, as there would be as much of the O_2 returned as CO_2, as there was O_2 taken in; for example—

$$\underset{\text{(Dextrose)}}{C_6H_{12}O_6} + 6O_2 = 6CO_2 + 6H_2O \quad \frac{6}{6} = 1.$$

On a *fat diet* the opposite condition exists: the fat molecule is poor in oxygen, and cannot supply from itself more than one-sixth of the amount required to oxidise the hydrogen to water; the remaining five-sixths have to be found from the incoming air, and in consequence less of the oxygen inspired is returned as CO_2. Thus:

$$\underset{\text{(Olein)}}{C_3H_5(C_{18}H_{33}O_2)_3} + 80O_2 = 57CO_2 + 52H_2O \quad \frac{57}{80} = 0{\cdot}71.$$

Consequently the R.Q. on a fat diet may be as low as 0·71. On a *protein diet,* which, in the matter of R.Q., comes midway between the carbohydrate and the fat diet, the oxygen in the molecule is still in insufficient quantities to oxidise its own hydrogen to water; and the elements other than carbon, such as sulphur, also require to be oxidised. It can contribute nearly half the amount required, but the remainder must be abstracted from the oxygen inspired. The R.Q. for protein varies, from circumstances which need not detain us here, but is generally taken at 0·8.

The R.Q. in animals depends, therefore, upon the nature of the diet: on one largely consisting of carbohydrates it approaches unity; on a diet of flesh it approaches the figure given for protein.

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* Not always so in the Tropics.

In herbivora the R.Q. is 0·9 to 1·0.
In carnivora the R.Q. is 0·75 to 0·8.
In omnivora the R.Q. is 0·87.

The value of the R.Q. lies in its being a measure of the oxidation occurring in the body as a whole. As a rule the amount of carbon dioxide formed is less than that of the oxygen absorbed, but there are exceptions to this, as in hibernating animals, where the processes of oxidation are at their lowest. In such cases the R.Q. shows the possibility of oxidation occurring without the production of carbon dioxide, and in other cases of carbon dioxide being formed without a sufficient absorption of oxygen to account for its production. Respiratory quotients as low as 0·3 have been found in hibernating animals, while during the period of their active life, when laying up or storing fat for winter use, the R.Q. may be greater than unity—even as high as 1·39. Such high quotients are not unknown among non-hibernating animals after a diet rich in carbohydrates, as in the case of fattening animals.

In these cases the carbon dioxide excreted is in excess of the oxygen absorbed. The carbohydrates are being stored up as fat, which is poor in oxygen; more oxygen is consequently rendered available from the food for the production of CO_2, which is split off from the carbohydrate molecule when converted into fat.

The R.Q. is not altered by muscular work, provided the work is not excessive or carried to the point of fatigue (see Table, p. 145). More oxygen is absorbed and more carbon dioxide given off during work, but the ratio is the same as during repose. The inference from this is that the material which is being used up by the muscles both during rest and during work is the same. With fatiguing work the R.Q. may fall, and this suggests that the body fat is being drawn upon.

In a starving animal the R.Q. diminishes, the creature lives on its own tissues, and as the body contains only a trifling amount of carbohydrate, it is on fat and protein that the animal lives. During starvation the output of carbon dioxide falls off at a greater rate than the consumption of oxygen.

There are **other gases returned from the lungs** besides oxygen and carbon dioxide, but very little is known about them. Both **hydrogen** and **marsh gas** are given off in the expired air of ruminants, having been absorbed by the bloodvessels of the intestinal canal. The amount has been placed at 3 litres (183 cubic inches) in twenty-four hours. The nitrogen of the air is returned unaltered.

Ventilation of the Lungs.—The lungs of an average horse contain, when fully distended, 42 litres (1½ cubic feet) of air, and at each inspiration 4 litres (250 cubic inches) are drawn in during a condition of repose. As the animal during repose breathes ten times a minute, the whole lung is ventilated about once a minute.

The column of air in the respiratory passages extends from the nostrils to the infundibular cavities. The air existing in the alveoli is spoken of as the **alveolar air**; it is the important air in respiration, and carries out the effective respiratory changes. From above the air-sacs to the nostrils is the '**dead space**'—that is to say, it contains air which is for the time being functionless from a respiratory point of view. The amount of the 'dead space' has not been determined for all animals; in man one-third of an inspiration fills it, while the remaining two-thirds go to the alveoli. This proportion must necessarily vary in different animals, depending on the length of the head and neck.

The composition of the air in the respiratory passages is obviously not the same throughout; it grows progressively poorer in oxygen and richer in carbon dioxide from nostrils to alveoli. During expiration the air from the dead space is the first to leave, and some of the alveolar follows. During inspiration the incoming air is diluted with that already in the lungs, and its chemical composition altered. If it takes a minute to ventilate the lungs—viz., to replace entirely the air they originally contained—it is obvious that, though some of the inspired air may reach favourably placed infundibular cavities at once, the bulk can reach them only gradually. In man it is estimated that about one-eighth of the alveolar air is changed at each respiration. How far an ordinary inspiration travels it is difficult to determine. Under the most favourable circumstances part of the axial stream of the current might reach the alveoli, especially those of the anterior lobes, but the greater part of it will get no farther than the bronchi. Some of this may effect deeper penetration at the next inspiration, while some of it will be expelled unchanged. In the infundibula the air is changed by the process of diffusion.

The composition of the air in the alveoli of the lungs has for years been a difficult question to determine, yet in order to explain pulmonary respiration this knowledge is essential. Haldane, to whom we are indebted for a method of obtaining the alveolar air, showed that in man the percentage of carbon dioxide is almost constant for the same individual, while the oxygen percentages are liable to great variation. The mean amount of carbon dioxide in alveolar air was found to be 5·16 per cent. in men; it was less in women. The total volume of air inspired is regulated by the amount of carbon dioxide in the arterial blood circulating through the respiratory centre, and the percentage in arterial blood is identical with that found in the air of the alveoli of the lungs.

During fast paces the respirations increase in frequency, and as they do so they decrease in depth. The actual bulk of an inspiration is less during fast paces than during repose, though the total amount of air respired in a given time is very much greater, owing to the increase in the number of respirations.

The influence of work on chest-ventilation in increasing the frequency and decreasing the depth of the respiration is dealt with on p. 143.

The Respiratory Exchange.—The respiratory exchange which takes place is of two kinds: an *external respiration* between the air and the blood through the medium of the lungs, and an *internal respiration* between the blood and the tissues. Both these are complex questions, and far from being settled.

We have seen that the air leaving the lungs has gained over 4 per cent. in carbon dioxide, and lost nearly 5 per cent. of its oxygen. The excess of oxygen absorbed over carbon dioxide produced is explained by the fact that oxygen is required for the purpose of oxidising not only carbon to carbon dioxide, but also hydrogen to water, and sulphur to sulphuric acid. In addition to the above changes, the expired air is found to be warmer than the inspired, and to be saturated with water vapour. This indicates a loss of body heat and likewise a loss of water. We have also learnt that in the alveoli of the lungs the composition of the air is not the same as in the dead space, and that in effect the air in the alveoli contains more CO_2 and less O_2. It is in the alveoli that the blood gets rid of its carbon dioxide, and takes up its oxygen, and this process must be examined in some little detail.

The **Gases of the Blood** are oxygen, carbon dioxide, and nitrogen. These may be extracted from the blood in the vacuum of a mercurial pump, or more conveniently by chemically expelling the oxygen by means of potassium ferricyanide, and the carbon dioxide by means of tartaric acid, and estimating their amounts. The proportion of gases found is liable to considerable variation, depending on the condition of the animal, the vessel from which the blood is drawn, the activity of the tissues, and even the length of time elapsing between collecting and analysing the sample.

The gases of venous and arterial blood are necessarily different. The figures given in the following table are only convenient averages, and represent the gases in 100 volumes of blood measured at 0° C. (32° F.), and 760 mm. (30 inches) barometric pressure:

	Oxygen.	Carbon Dioxide.	Nitrogen.
Arterial blood - - -	20	43	1·2
Venous blood - - -	12	50	1·2

Blood, in passing from arterial to venous, loses 8 parts of oxygen and gains 5 parts of carbon dioxide, the nitrogen remaining unchanged. This suffices as a broad general statement, but for the purpose of ascertaining the respiratory changes in the blood, the mixed venous blood of the body—viz., that found in the right ventricle of the heart—should be examined. An analysis of this, from the dog, compared with arterial blood, is given in the following table:

Venous Blood from Right Ventricle.			Arterial Blood.		
Oxygen.	Carbon Dioxide.	Nitrogen.	Oxygen.	Carbon Dioxide.	Nitrogen
Mean. 11·9 { 16·6 5·5	Mean. 44·3 { 47·5 38·8	Mean. 2·0 { 4·01 1·32	Mean. 19·2 { 23·3 15·0	Mean. 38·8 { 43·1 34·8	Mean. 2·7 { 5·50 1·62

The mean and the extremes are shown in the above table, which gives a good idea of the variations in the amounts of gases especially in venous blood; and this variation doubtless holds good for all animals. Both nitrogen and argon are found in blood. It is believed they are in simple solution and of no physiological value.

Oxygen in the Blood.—If the oxygen in blood were held in simple solution, as it is in water, and the blood introduced into a mercury pump, with every reduction of pressure in the pump oxygen would be given off from the blood. But in effect this is not so. It is not until the pressure in the pump stands at one-third of an atmosphere that oxygen begins to escape, and when the pressure is reduced to one-sixth of an atmosphere, the oxygen is suddenly and vigorously liberated. It is evident that its union with something has been suddenly broken, and this something is hæmoglobin. Further evidence that the oxygen is not simply absorbed by blood is afforded by the experiment of shaking air and blood, and oxygen and blood, together. The blood absorbs more oxygen from the air than an equal bulk of water would, while it absorbs no more from an atmosphere of pure oxygen than it does from atmospheric air. The explanation is that the oxygen and hæmoglobin form a definite chemical compound.

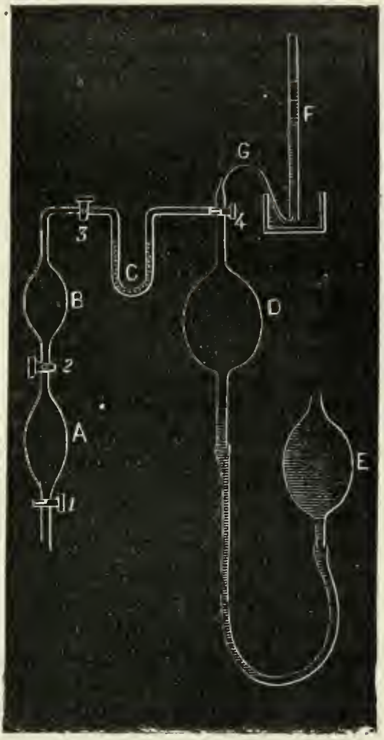

FIG. 43.—SCHEME OF GAS PUMP.

A, The blood-bulb; B, the froth-chamber; C, the drying-tube; D, fixed mercury bulb; E, movable mercury bulb connected by a flexible tube with D; F, eudiometer; G, a narrow delivery tube; 1, 2, 3, 4, taps, 4 being a three-way tap. A is filled with blood by connecting the tap 1 by means of a tube with a bloodvessel. Taps 1 and 2 are then closed. The rest of the apparatus from B to D is now exhausted by raising E, with tap 4 turned so as to place D in communication with G only, till the mercury fills D. Tap 4 is now turned so as to connect C with D, and cut off G from D, and E is lowered. The mercury passes out of D, and air passes into it from B to C. Tap 4 is again turned so as to cut off C from D, and connect G and D. E is raised, and the mercury passes into D, and forces the air out through G, the end of which is not yet placed under F. This alternate raising and lowering of E is continued till a manometer connected between C and 4 indicates that the pressure has been sufficiently reduced. The tap 2 is now opened. The gases of the blood bubble up into the froth-chamber, pass through the drying-tube C, which is filled with pumice-stone and sulphuric acid, and enter D. The end of G is placed under the eudiometer F, and by raising E, with tap 4 turned so as to cut off C, the gases are forced out through G and collected in F. The movements required for exhaustion can be repeated several times till no more gas comes off. The escape of gas from the blood is facilitated by immersing the bulb A in water at 40° to 50° C.

The available oxygen in blood is carried in two forms: a very small quantity, amounting to 0·65 volumes per cent., is simply dissolved in the plasma; the other and larger portion is the oxygen chemically combined with hæmoglobin, which may be conveniently taken at 20 volumes per cent. As fast as the oxygen in free solution is used up by the tissues it is replaced in the plasma by the oxygen contained in the hæmoglobin of the red cells, for the reason that hæmoglobin is an easily dissociated* compound and readily gives up free oxygen. The dissociation of oxygen in the blood from the hæmoglobin is very rapid, and occurs in about one second; similarly, the taking up of oxygen in the vessels of the lungs by the hæmoglobin is equally rapid.

When a pure solution of hæmoglobin is exposed at body temperature to a mixture of oxygen and nitrogen, the percentage saturation of the hæmoglobin with oxygen will increase with a rise in the oxygen pressure in the following order:

Partial Pressure of Oxygen in Mm.	0	5	10	20	50	100
Percentage of oxyhæmoglobin - -	0	37	55	72	87	94

This is graphically represented in Fig. 49, Curve 0. In the circulating blood itself the conditions are different from a pure solution of hæmoglobin, the main disturbing factor in the former being the carbonic acid pressure. In the presence of a carbonic acid pressure of 40 mm. Hg, the blood loses its oxygen rapidly whenever the oxygen pressure falls below 50 mm., while in the absence of carbonic acid, even when the oxygen pressure has fallen to 20 mm., the percentage of oxyhæmoglobin still remains very high (80 per cent.). The effects produced by varying the carbonic acid pressures are shown clearly in Fig. 49.

Under certain pathological conditions there is a defective saturation of the arterial blood with oxygen, designated by Haldane† **anoxæmia**, or insufficient supply of oxygen to the tissues, and among other causes of this condition he points out that, when the partial pressure of the carbonic acid in the blood is diminished, the dissociation of hæmoglobin is diminished in consequence of the hæmoglobin holding on more tightly to its oxygen. It has already been pointed out that the facility with which hæmoglobin parts with its oxygen is likewise affected by the presence of certain salts in the blood, and these act as carbonic acid acts—*i.e.*, by means of their acidity.

The facility with which hæmoglobin parts with its oxygen is affected by the temperature, for under a given pressure less oxygen is taken up by hæmoglobin the higher the temperature.

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* The process termed *dissociation* may be defined as the tendency which certain gases have to leave the substances with which they are united when the surrounding pressure becomes reduced. In the animal body it is not confined to the union of oxygen with hæmoglobin. The same process is at work in liberating the carbon dioxide in the lungs from the bodies with which it is chemically combined.

† *British Medical Journal*, July 19, 1919.

The blood in the lungs comes into contact with the air in the alveoli, the oxygen pressure of which is 100 mm. of mercury, or about 13·2 per cent. of an atmosphere; there the hæmoglobin becomes nearly saturated (93 per cent.) with oxygen. The blood returns to the arterial system and enters the capillaries with 20 volumes of oxygen per cent. at a partial pressure of 100 mm. It leaves the tissues in a second or two with only 12 volumes of oxygen, having yielded up 8 volumes, or 40 per cent., of its original amount, in consequence of the fact that the partial pressure of oxygen in the tissues is practically nil. Dissociation of the oxyhæmoglobin has therefore occurred, and undoubtedly this has been assisted by the presence of carbon dioxide (see Fig. 49). The oxygen which has passed into the tissues is that in free solution in the blood, and the loss of this is at once restored by the passage of oxygen from the hæmoglobin of the red cells into the plasma.

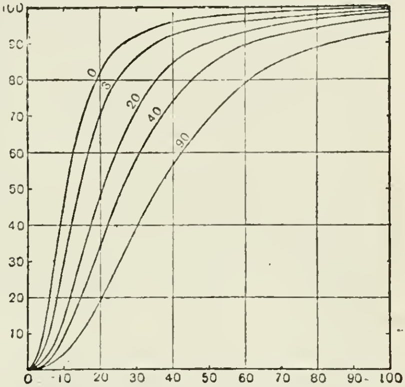

Fig. 49.—Dissociation Curves of Blood at 37° (Barcroft).

The curves show the effect produced on dissociation by a rise in CO_2 pressure, the blood having been exposed to the different oxygen pressures.

(1) With no carbonic acid - - 0
(2) With CO_2 at 40 mm. pressure - 40
(3) With CO_2 at 90 mm. pressure - 90

Abscissæ = O_2 pressure in mm. of Hg.
Ordinates = Percentage of Oxyhæmoglobin.
(Barcroft.)

Taking advantage of the fact that only a trifling percentage of the oxygen in blood is dissolved, while the bulk is chemically combined, Haldane was able to show that the oxygen capacity of the blood varied with the colouring power, and thus established a method of clinically estimating the hæmoglobin in any sample.

Carbon Dioxide in Blood.—This gas is held in blood both in simple solution and in chemical combination, the latter accounting for the larger part of the contained gas. In a gas-pump the blood gives up all the carbon dioxide it contains; but if, instead of using blood, serum be so extracted, it is found impossible to obtain the whole of the carbon dioxide from the latter without the use of an acid. It has been generally accepted in the past that carbon dioxide in blood is carried by the sodium bicarbonate. According to Buckmaster sodium bicarbonate takes practically no share in the process; he considers that carbon dioxide is mainly carried by the hæmoglobin, being united to the protein portion of the molecule, thus leaving unaffected the iron moiety by which the oxygen is carried. Hæmoglobin is capable not only of absorbing large quantities of carbon dioxide, but of giving it off in the lungs by dissociation. The amount taken up by hæmoglobin is one-tenth greater when the hæmoglobin is reduced than when it is saturated with oxygen, so that venous blood takes up more than arterial at the same partial pressure.

The amount of carbon dioxide in venous blood is about 46 volumes per cent., of which about 5 per cent. is in solution; but the fluid is not saturated, for it can be shown that blood will dissolve as much carbon dioxide as water which at normal temperature and pressure is about 100 per cent.

The source of the carbon dioxide is the blood in the tissues, where it arises as the result of oxidations. By its presence in blood the normal reaction of that fluid is preserved. It is also the normal stimulus to the respiratory centre, and it insures the liberation of oxygen from the hæmoglobin. This explains why venous blood takes up more oxygen than arterial at the same partial pressure. These effects are produced by virtue of its acid properties.

Circumstances influencing Respiratory Exchange.—Respiratory exchange is influenced by food, being not merely increased as the result of the considerable muscular effort involved during mastication, but directly excited by the nature of the food. Thus maize causes in horses a greater excretion of carbon dioxide and absorption of oxygen than an equal weight of oats. A protein diet causes a larger respiratory exchange than one of carbohydrate or fat. Respiratory exchange is greater in the young than in the old, less during sleep than when awake, greater in warm-blooded than in cold-blooded animals, greater in small than in large animals, and greater at work than at rest. Some of these points will be examined at length in the chapter devoted to their consideration.

The Tension of the Gases in the Blood.—In order to arrive at a knowledge of the laws which govern the exchange of carbonic acid and oxygen between the alveolar air and the pulmonary capillary blood, it is necessary to determine the tension of these gases in the blood. If a gas mixture containing definite quantities of oxygen, carbonic acid, and nitrogen were brought into contact with a thin film of blood at body temperature, and if it were found that, after sufficient time for the establishment of gaseous equilibrium had been given, the composition of the gas mixture remained unaltered, then one might conclude that the tensions of the gases in the blood corresponded to their partial pressures in the gas mixture. Instruments, called aerotonometers, have been used to determine the gas tensions in this way. The partial pressure or tension of the oxygen is highest in the alveolar air and lowest in the tissues, while the carbonic acid is highest in the tissues and lowest in the alveolar air, the differences in the former case being great—namely, from about 14·5 per cent. of an atmosphere (110 mm. Hg.) in alveolar air to zero in the tissues, and in the latter much less marked—namely, from about 8 per cent. of an atmosphere in the tissues (60 mm. Hg) to slightly over 5 per cent. of an atmosphere (40 mm. Hg) in the alveolar air. The tensions of the gases in the blood and in the tissues vary, but the following table gives an approximate idea of the pressures which occur in the important situations.

TENSIONS OF GASES.

	Oxygen.	*Carbonic Acid.*
	Mm. Mercury.	Mm. Mercury.
Alveolar air - - - -	110	↑ 40 −
Arterial blood - - - -	100	40 +
Venous blood - - - -	40	45
Tissues - - - - -	0 ↓	60

Gaseous Exchange in the Lungs.

There are two theories put forward to account for the transfer of oxygen from the external air to the blood, and the passage of carbon dioxide from the blood to the external air. The first and oldest view is a physico-chemical one. If the partial pressure of the oxygen in the air-cells is higher than in the blood, oxygen will pass into the blood. If the pressure of the carbon dioxide in the blood is greater than in the alveolar air, carbon dioxide will be given off to the latter. Until recent years the acceptance of this explanation had been very general. When, however, the air in the alveolar cavities was examined, facts were discovered which threw grave doubt on the accepted view. It was found by certain observers that the pressure of oxygen in the arterial blood might be above that of the oxygen in the alveoli, and that the pressure of the carbon dioxide in the blood might be below that in the pulmonary alveoli. Under these circumstances it was held that the theory of diffusion was no longer able to explain the respiratory exchange in the lungs, and a fresh explanation had to be found. The view held by those who reject the physical theory is that the respiratory exchange is carried out by a process of secretion, and this in the present state of our knowledge of physics and chemistry is very difficult to understand. We must look at both views more closely.

The diffusion theory is outlined above. The blood, robbed of

40 per cent. of its oxygen in the tissues, and carrying over 16 per cent. increase of carbon dioxide, makes its way back to the lungs in a partially reduced condition. Here it circulates through the vast capillary system spread over the alveoli of these organs, and is brought as closely as possible into contact with the alveolar air in the ultimate air-passages. Nothing but the capillary wall and the delicate moist membrane of the alveolus separates the blood from the air, and through this wall the oxygen instantaneously passes, in consequence of its partial pressure in the blood being low and in the alveoli high. In the blood it is taken up by the plasma, and then absorbed by the hæmoglobin of the red cells, with which, as we have already seen, it forms a weak chemical compound. Concurrently with this, carbon dioxide, by the process of diffusion, passes out of blood, in which its partial pressure is high, into the air of the alveoli, where its partial pressure is low.*

We have said that for some time past the law of diffusion and chemical dissociation has been held by some authorities inadequate to explain the pulmonary exchange, the reason being that there are many observations, none of which, perhaps, are entirely free from error, which go to show that the alveolar air may contain a higher partial pressure of carbon dioxide than is found in the blood, while the oxygen tension of the alveolar air may be below that of the blood. Under these circumstances it is held that oxygen is secreted.

It is no part of a work of this character to examine the rival physical and vital theories of pulmonary respiration, but no matter how difficult it may be to explain the secretion of oxygen, the fact remains that it occurs in fishes.

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* If a mixture of gases be absorbed by a fluid, it is found that the volume of each gas forming the mixture is absorbed as perfectly as if it were the only gas present; no more and no less is absorbed, whether the gas be alone or whether it form only a proportion of the mixed gases present. This is explained as resulting from the fact that one gas does not exercise any pressure upon the other gases with which it forms a mixture. The term used by Bunsen to define the pressure exerted by one gas in a mixture of gases is '*partial pressure.*' For example, 100 volumes of air contain at freezing-point 0° C., and standard barometric pressure 760 mm. (30 inches), 21 volumes of oxygen and 79 volumes of nitrogen. What is the partial pressure exerted by each gas in this mixture?

$\frac{760 \times 21}{100} = 159{\cdot}6$ mm. (6·3 inches) of mercury; which is the partial pressure of the oxygen;

and

$\frac{760 \times 79}{100} = 600$ mm. (23·7 inches) of mercury, the partial pressure of the nitrogen.

The term 'partial pressure' occurs so constantly in all discussions of the nature and causes of gaseous exchanges of the animal body, that the above explanation has been given to make the matter clear. The term *tension* is employed when the gases are dissolved, *pressure* when they are in the gaseous state.

The so-called 'swim bladder' of deep-sea fishes contains a high percentage of oxygen. Cods brought up from a depth of 45 feet have shown 52 per cent. of oxygen in their gas reservoir, and gas drawn off on succeeding days has shown 79 per cent. and 84 per cent. of oxygen in the bladder. The production of this gas by secretion is the only possible explanation of its existence. As a matter of fact, there is a vascular area in the swim bladder by which it is formed; and to render the secretory theory more complete, nerves supplied by the vagus have been found, which on section prevent the further accumulation of gas.

In the researches of Haldane and Priestley the alveolar air was found to contain a remarkably constant percentage of carbon dioxide. This constancy is maintained by the increase in alveolar ventilation, which results from the increased production of carbon dioxide. The respiratory centre, these observers discovered, is exquisitely sensitive to the slightest increase in the alveolar carbon dioxide pressure, a rise of 0·2 per cent. of an atmosphere being sufficient to double the amount of alveolar ventilation during rest. It is an astonishing fact that the lungs should be able to arrange for their effective ventilation.

Internal or Tissue Respiration.—This is infinitely more obscure than pulmonary respiration—in fact, the means by which the tissues utilise the oxygen given to them is quite unknown.

We have previously seen that in the passage of blood through the capillaries of the tissues it loses in about one second 40 per cent. of its oxygen. This loss occurs in consequence of the dissociation of the oxyhæmoglobin in the presence of tissues whose oxygen tension is practically *nil.* The blood, when it left the pulmonary capillaries, was nearly saturated with oxygen; it held, perhaps, 19 c.c. of oxygen for every 100 c.c. of blood, equal to a partial pressure of 100 mm. of mercury. In the tissues, the oxygen being used up or fixed by living substance as fast as it is supplied, its partial pressure is *nil.* Under these circumstances, there is no difficulty in accounting for the transfer of oxygen from the blood to the tissues on purely physical and chemical grounds, the dissociation of hæmoglobin being assisted by the presence of carbon dioxide in the tissues, for, as previously mentioned, it is known that an increased tension of carbon dioxide in blood favours the giving up of oxygen to the tissues.

It is evident, in consequence of the above changes, that there is a reduction in oxygen tensions from the blood to the tissues; the tension being highest in the blood-cell, is less in the plasma, still less in the vessel wall, lower in the lymph, and at its lowest in the tissue elements. In fact, these various tissues deal with the hæmoglobin in order to obtain its oxygen, exactly in the same manner as we deal with it outside the body in order to obtain its gases—viz., expose it to reduced pressure, as, for example, in a mercurial pump. The blood, as we have mentioned earlier, does not give up all its oxygen in the tissues, probably on account of the rapidity of its passage. On no occasion, excepting under the condition of asphyxia, is the whole of the hæmoglobin reduced. There may be more oxygen returned to the lungs unused than has been abstracted by the tissues.

The whole of the carbon dioxide in blood is not got rid of in the lungs; the tension of the gas in arterial blood on leaving the pulmonary capillaries is equal to 5 per cent. of an atmosphere or 35 mm. of mercury. On the other hand, the pressure of carbon dioxide in the tissues is high—50 mm. to 70 mm. In consequence, there is no difficulty in explaining on physical and chemical grounds the transfer of carbon dioxide from tissues to blood.

The medium in which this transfer occurs is the lymph which bathes the tissues. This is the carrier between the blood and the cell, for it is in the cell that tissue respiration occurs, and not in the blood.

As evidence of the important fact that the oxidations take place in the tissues, and not in the blood, two interesting experiments may be quoted. If the blood in a frog's body be replaced by saline solution, and the animal kept in an atmosphere of pure oxygen, it will continue to produce carbon dioxide. It is obvious in this case that the carbon dioxide has been produced from the tissue, as the animal is without blood. A more telling experiment is the following: Methylene blue is a comparatively stable oxygen-holding substance—more so than oxyhæmoglobin—and is likewise an extremely powerful dye. If a solution be injected into the circulation and the animal destroyed, the blood is found dark blue in colour, but the tissues, especially the muscles, are normal in appearance. When, however, they are exposed to the air, they turn a vivid blue. The explanation is that the tissues robbed the methylene blue of oxygen, and formed a colourless reduction product, which on exposure to the air took up oxygen and again formed methylene blue. No more remarkable example of the instantaneous absorption of oxygen by the tissues could be furnished.

In spite of the imperative need for oxygen which exists in the body, it is remarkable how little can be obtained from it. From muscle none can be obtained; from the various secretions—lymph, bile, urine, milk, saliva—only a very little can be obtained, though in all these there is an abundance of carbon dioxide.

In the respiration of muscle, which can be readily studied, the muscle preparation of a frog will go on contracting until exhausted in an atmosphere of hydrogen, producing all this time carbon dioxide, thereby showing that it is using oxygen, yet neither in the muscle nor in the atmosphere surrounding it does any oxygen exist. The question, therefore, is, How does the oxygen-free muscle obtain oxygen for the production of carbon dioxide? Few things in the whole range of physiology are more difficult to understand, but it is supposed by some that when the oxygen reaches the muscle it is at once stored up in a compound or compounds among the muscle molecules; hence the substance used by the muscle has been termed intramolecular oxygen. In this connection it is important to note that Bayliss reminds us that there is no experimental evidence of the existence of intramolecular or other form of cellular oxygen available for oxidation. The changes which the oxygen undergoes from the time it leaves the blood until it reappears as carbon dioxide in the tissues are completely unknown. It has been suggested that the nature of the oxidative changes occurring in living tissues may be due to the presence of oxidising ferments in the body—*oxydases*, as they have been termed. Such ferments have been demonstrated to exist in nearly all the tissues.

The phenomena of tissue respiration may be studied in living tissues by ascertaining the composition of the blood before and after circulation through them. Such an experiment has been carried out on the horse by Chauveau and Kaufmann, who utilisedthe levator muscle of the upper lip during feeding. The consumption of oxygen and the production of carbon dioxide was many times greater during activity than during rest. Glands such as the submaxillary have been similarly examined, while the respiratory changes occurring in the lungs during rest and work have formed the subject of many experiments. All furnish the same evidence, though not all with the same clearness. One remarkable example of tissue respiration is furnished by L. Hill's examination of the respiratory exchange in the living brain, which, compared with that in skeletal muscle, was found to be very low.

It is impossible here to examine further the question of respiration in the tissues, but the matter will be referred to in detail when its importance warrants it, as in respiratory exchange, muscular work, animal heat, and general body metabolism.

Deficiency in Oxygen.—When an animal is compelled to breathe the same air over and over again, there is a gradual loss of oxygen and an increase in carbonic acid, and though death will ultimately ensue unless the air be renewed, it is remarkable that before this occurs nearly the whole of the oxygen will have been consumed from the atmosphere. This is further evidence, if any be needed, that the oxygen is not simply absorbed by the blood, and that its absorption does not obey the ordinary laws of pressure. Experimental inquiry has proved that animals may live in an atmosphere containing only 14 per cent. of oxygen, that distress appears at 11 per cent., for at or below this pressure the hæmoglobin cannot take up its full amount of oxygen, and that rapid asphyxia follows when the oxygen falls to 3 per cent.

In poisoning by carbon monoxide, the latter gas turns the oxygen out of the blood-cells, yet although the whole of the red cells are converted into carriers of carbon monoxide, the animal may still be kept alive in an atmosphere of pure oxygen under pressure, the amount of oxygen in solution in the plasma at an oxygen pressure of two atmospheres being sufficient to carry on the functions.

We have already referred to Haldane's recent work on deficiency of oxygen in the tissues designated **anoxæmia.** He points out that this condition may be brought about by defective saturation of the arterial blood with oxygen; by a slowing of the circulation, so that an excess of oxygen is used up in the tissues; by a defective proportion of hæmoglobin in the blood, and by alterations in the dissociation of oxyhæmoglobin, so that oxygen is given off less readily to the tissues.

When the supply of oxygen to the tissues is less than their requirements, there is an increase in the number of respirations, which has the effect of bringing in more oxygen and getting rid of the excess of carbon dioxide in the lungs. Where, however, carbon dioxide is not in excess, the increased respirations wash out an abnormal amount of this gas, and so increase the trouble by removing from the body the natural acid stimulus to the respiratory centre. The blood becomes abnormally alkaline in anoxæmia, and the condition known as **alkalosis** is produced. In this state the liver and kidneys respond by getting rid of alkali. In connection with alkalosis it is convenient to refer to **acidosis**, which, until recently, was believed to be associated with a deficiency of oxygen. Haldane at one time thought that, owing to this deficiency, lactic acid was produced in the body and remained in the blood, thus helping to stimulate the respiratory centre. This hypothesis he no longer believes to be necessary.

Hyperpnœa is the term applied to the slightly increased amplitude and frequency of the respiratory movements, such as occur in gentle exercise, as the immediate result of any commencing defective oxygenation of the blood, or of other cause which acts as a stimulus to the respiratory centre. When the stimulus is strong or continued, a further increase in the force and frequency of the respiratory movements takes place, and this condition is known as **dyspnœa.** The later stage of dyspnœa is characterised by the respiratory movements becoming 'convulsive' in their activity, and this finale to dyspnœa marks the onset of true asphyxia.

If the air supply be entirely cut off, asphyxia and death rapidly ensue. **Asphyxia** has been divided into three stages. In the first the attempts at breathing are laboured and painful, deep and frequent, and all the respiratory muscles, including the supplemental ones, are brought into play. Convulsions occur, and the blood-pressure rises. In the second stage the inspiratory muscles are less active, the expiratory still powerful, and the convulsions cease. In the third stage the animal lies unconscious, occasional violent inspiratory gaspings occur, the mouth is open (even in the horse), the pupils dilated, the pulse barely perceptible or absent. During this stage the blood-pressure rapidly falls. Death occurs in from five to six minutes from the commencement of the first stage. Young animals are less easily asphyxiated than adults for the reason that their tissue respiration is much less. The length of time necessary to drown puppies and kittens is evidence of this, and they may recover even after prolonged immersion.

Excess of Oxygen.—It has been shown that oxygen above a certain pressure is very poisonous. From 3 to 5 atmospheres of oxygen, corresponding to 15 to 25 atmospheres of air, suffice to kill seeds, to hinder the development of eggs, and to produce convulsions in warm-blooded animals. In these latter cases the amount of extra oxygen in the blood is 10 volumes, so that there are 30 instead of 20 in every 100 volumes of blood. This extra oxygen is not carried in the red cells, but in solution by the plasma. All animals are instantly killed by a pressure of 50 atmospheres of oxygen. The reason of the toxic nature of oxygen at high tensions is unknown. The blood cannot, by our increasing the amount of oxygen above that contained in air, be made to take up much more oxygen than if the normal amount only were present. A pressure of 10 atmospheres causes an increase of only 3·4 per cent. absorbed, so that the blood contains 23·4 per cent. of oxygen instead of 20 per cent. The practical application of this fact in the treatment of certain diseases by the inhalation of oxygen is interesting. If we double the amount of oxygen in the air, less than 1 per cent. of the extra addition is absorbed. Either the small amount of extra oxygen thus absorbed must be very valuable, or we must find some other explanation of the undoubted advantage of oxygen inhalation in disease.

The physiology of the matter is, in effect, this: The air contains 20 per cent. of oxygen, which is more than enough for the needs of the body; even the venous blood returns to the lungs with from 10 to 12 volumes of oxygen per cent. unused; and if the oxygen in the air be doubled, less than 1 per cent. of the extra is absorbed. It may, however, be that the excess of oxygen in the alveolar air of the lungs during oxygen inhalation enables the tissues to obtain their normal amount more easily. Oxygen inhalation is of special value when the barometric pressure is very low or the pulmonary absorbing surface is diminished.

Apnœa is the term applied to a condition in which no respiratory movements of any kind are made. It is in the main a condition artificially produced in the laboratory, though it may also be met with in surgical operations. Apnœa may be produced artificially by blowing air into and sucking it out of the lungs at a more rapid and forcible rate than the ordinary respiratory rhythm of the animal. Two conditions have now been brought about, either of which separately will produce apnœa. In the first place, there is a very free lung ventilation, and in consequence a change in the composition of the gases in the alveoli of the lungs, and so in the blood of the medulla. Secondly, the partial pressure of the carbon dioxide in the blood will be lowered, and as a result of the natural stimulus of the respiratory centre being withdrawn, the centre will remain inactive. This is not due, as was at one time supposed, to an excess of oxygen in consequence of free lung ventilation, as it will occur when the lungs are distended with hydrogen.

If the lowered pressure of carbon dioxide in the blood is the cause of the suspended breathing, the introduction of this gas into the blood should abolish the apnœic condition. This is found to be so. A blast of carbon dioxide cuts short apnœa in the rabbit, while a blast of air has no such effect.

Apnœa may also be produced in another way, by stimulation of the afferent pulmonary fibres of the vagus by the repeated distension of the lungs. This condition cannot be produced if the vagi be divided.

The real value of the experimental production of apnœa lies in the light which it throws on the normal respiratory process, and it is very remarkable that the normal rate of breathing suitable to the animal's immediate requirements should be regulated by the carbon dioxide circulating through the medulla.

There is a surgical condition known as **shock,** common after prolonged operations or excessive hæmorrhage. In these cases there are a diminished amount of carbonic acid in the blood, a dangerous fall in blood-pressure, and a deficient oxygen supply. With this last is associated the production of lactic acid, and acidosis has been considered to be present. The view held at the present time is that no acidosis is present, as it would be neutralised by the sodium bicarbonate of the blood, and that the symptoms are due to diminished bulk of fluid in circulation and a deficient oxygen supply. In connection with the diminution in the total volume of blood, Bayliss showed that a solution of gum arabic in 0·9 per cent. saline remained in the vessels, and was capable of saving many lives, while ordinary saline only acted temporarily, and rapidly passed through the vessel wall into the tissues. Intravenous injections of gum together with oxygen inhalation constitute the modern method of dealing with surgical shock.

The Nervous Mechanism governing Respiration.—A large number of nerves is required for the production of respiratory movements. The facial dilates the nostrils, the vagus supplies the larynx, the phrenic the diaphragm, certain spinal nerves supply all the muscles of the trunk engaged in respiration, and besides these nerves with purely motor functions, there is an enormous number of sensory nerves connected with respiration. Such extensive ramifications require for the proper discharge of their functions a central co-ordinating mechanism, and this is known to exist in the medulla. The position of this centre has in certain animals been very accurately defined, though it is not represented histologically by any special group of cells. In general terms it may be spoken of as being situated close to the deep-seated origin of the vagus, and in front of the vasomotor centre. The fibres which pass from it down the cord end in motor nuclei in the grey matter of different levels, corresponding to the points of outflow of the nerves connected with the muscles of respiration. There is also evidence of decussation of the fibres, or at any rate of a connection between those on the right and left sides of the cord, as we shall see presently in dealing with the phrenic.

The respiratory centre consists of two halves, each of which is capable of working independently. By some it has also been considered to consist of two parts—an expiratory and inspiratory. There is no definite indication of the former division, but the latter is well marked. Of the two acts, the inspiratory is the more important, for, as we have already seen, expiration may, under some circumstances, be a purely passive act. Nevertheless, there are special expiratory functions of central origin, such as the act of straining, as in parturition, micturition, defæcation, or coughing—actions which are certainly not of a passive character, and which might be considered to originate in a special expiratory centre.

It is known that, besides the motor nerves previously described as being connected with the process of respiration, the respiratory centre is connected extensively with sensory nerves—probably with every sensory nerve in the body, for the centre may be readily stimulated through any sensory branch. Further, the cortex of the brain is connected with the respiratory centre, for the animal may at will increase or withhold its respiration, while psychical events produce their effects through some such channel, as may be witnessed in the increased respiration of nervous apprehension. A perfectly orderly sequence of events occurs in normal respiration, beginning at the nostrils and ending at the flank, the entire smoothness and regularity of which is dependent on the nervous connections of the respiratory centre with the outside.

The centre is automatic, *i.e.*, it is within itself that the discharges are generated which issue forth as respiratory impulses; indeed, it is as automatic in its working as the heart, for if every nervous connection leading to it be divided, the centre continues notwithstanding to act rhythmically. If the chief path by which these impulses gain the exterior be interrupted—as, for instance, by dividing the spinal cord behind the medulla—death from paralysis of respiration at once ensues. Such a section does not affect the facial muscles of respiration, and an animal that has ceased to breathe and is virtually dead may still continue to make powerful inspiratory facial gasps, the nerves supplying these muscles being derived from a point anterior to the section.

The nature of the impulses which issue from the respiratory centre depends upon the character of the impulses received from without, which stimulate their production reflexly. Thus the breathing may be hastened or slowed down, quickened in rhythm and decreased in depth, or increased in both rhythm and depth. From the cortex of the brain impulses may be transmitted, voluntarily increasing the respirations, as in sniffing, or withholding them entirely, as when the head is under water. Through the medium of the nasal branch of the fifth pair of nerves impulses may be transmitted from the nostrils inhibiting inspiration; from the skin impulses of two kinds are received—viz., those increasing and those diminishing respiration. It has even been supposed that different nerve fibres are concerned in the transmission of stimulating and inhibiting impulses to the respiratory centre, though these are not exclusively channels for respiratory purposes. From the larynx through the superior laryngeal nerves impulses inhibiting inspiration and stimulating expiration are transmitted, and similarly impulses are sent through the sensory fibres of the glosso-pharyngeal, which inhibits respiration at the moment of swallowing. In the diagram (Fig. 50) the chief nervous connections of the respiratory centre are shown; the sign denotes whether they convey impulses which stimulate or inhibit the respiratory centre.

The Influence of the Vagus on Respiration.—The vagus is the most important afferent channel by which the lungs are brought into connection with the medulla; the sensory fibres are distributed over the area from the glottis to the alveoli of the lungs. If impulses from the lungs to the medulla are cut off by dividing the vagi, the respirations become slower and deeper (Fig. 51, C); in the horse they have been known to fall to five per minute; the inspirations particularly are deep and prolonged. If one vagus only be cut, the effect just described may not occur, or be of only a partial character. From this it is evident there are impulses passing up the vagus from the lungs to the medulla which maintain the normal respiratory rhythm, and these are permanently lost by section of the nerves. If the end of the divided vagus which is connected with the brain be stimulated

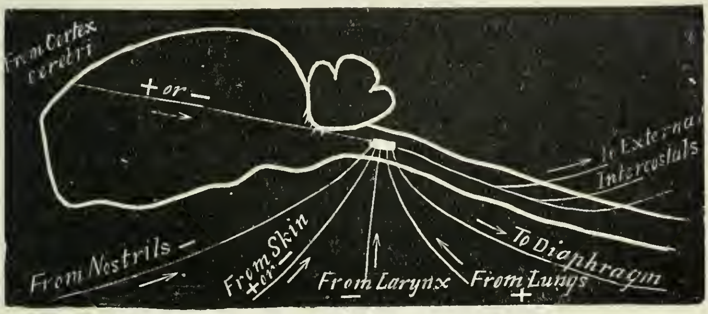

FIG. 50.—DIAGRAM TO ILLUSTRATE THE CHIEF NERVOUS CONNECTIONS OF THE RESPIRATORY CENTRE (AFTER WALLER).

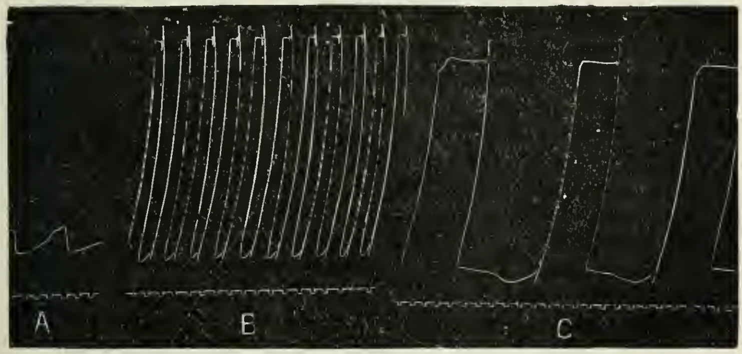

FIG. 51.—RESPIRATORY TRACINGS: DOG (STEWART).

A, Normal; B, effect of stimulation of the central end of vagus; C, effect of section of both vagi. Time-tracing, seconds.

below the origin of the superior laryngeal nerve, there is arrest of respiration if the stimulation be strong, but with moderate stimulation respiration is quickened (Fig. 51, B). The strength of the stimulating current and the condition of the centre at the time of the experiment appear to be important factors in determining the exact results which will follow. But the interpretation of the results of these experiments shows that there are two kinds of fibres in the vagus conveying impulses from the lungs to the medulla, and affecting it in opposite ways: (1) Fibres carrying impulses which cause inspiration and inhibit expiration; and (2) fibres conveying impulses which inhibit inspiration, and so cause expiration. These sets of fibres are in alternate activity, and the cause of their normal stimulation is believed to be the alternate distension and collapse of the air vesicles. If, for example, air be pumped into the lungs, expiration is excited, and if it be sucked out, inspiration follows; from which it is argued that an inspiration, by distending the air vesicles, excites expiration, and the contraction of the air vesicles on expiration excites inspiration. It can be shown experimentally that electrical changes in the divided vagus indicate a current of a particular character throughout each inspiration, and another of a different character during expiration. If, however, the respiratory centre be regarded as primarily automatic, the inspiratory fibres found in the vagus may be regarded as increasing the rate of respiration, the expiratory as inhibiting or controlling inspiration, and thus producing expiration. If this view be adopted, the act of inspiration proceeds from an automatic centre, which requires no other stimulus than that which is generated within itself, while expiration proceeds from the stimulation caused by distension of the air vesicles.

The nature of the internal stimulus which provokes the respiratory centre has for some time been the subject of controversy. All were agreed that the stimulus lay in the blood gases, but whether this was to be attributed to their richness in carbon dioxide or to their poverty in oxygen could not for some time be decided. It is now generally admitted that the richness in carbon dioxide is a more potent stimulant than the poverty in oxygen, and Haldane's and Priestley's researches show the extraordinary delicacy of the respiratory centre's response to minute increases in carbon dioxide, a 0·2 per cent. increase leading to an increased pulmonary ventilation of 100 per cent. It should be noted that it is not the carbon dioxide in the venous blood which stimulates the medulla, but that which is in the arterial blood.

During muscular work, especially that of a severe nature, there is lactic acid in the circulating blood. To this condition the term **acidosis** is applied, but in Haldane's recent work he points out that lactic acid is rapidly oxidised in the system, and that his earlier interpretation of the influence of this acid in stimulating the respiratory centre cannot now be held to be true. Should blood become slightly too acid, the liver produces ammonia instead of urea, which neutralizes the acid and is excreted by the kidneys as the ammonium salt.

Respirations are increased in frequency as the result of such sensory stimulation as occurs, for instance, in painful operations; sensory stimulation of the abdominal wall may be employed as a means of starting an inspiration in chloroform-poisoning.

Animals which do not sweat, pant after work in order to get rid of the surplus heat by warming a larger volume of air. This question will be considered again under Animal Heat, but the possible mechanism involved may here be glanced at. It is conceivable that the congested condition of the skin may send impulses to the respiratory centre, but this will not account for the panting of animals in 'show condition.' Here there is presumably no increase in the carbon dioxide in their alveoli, and the stimulation to increased respiratory activity would appear to be obtained reflexly from the skin, though the increased temperature of the circulating blood in the medulla may account for it, as appears to be the case in fever.

Influence of the Phrenic Nerves on Respiration.—The phrenic is essentially an inspiratory nerve. We have referred to the cutting off of the respiratory centre by dividing the cord above the phrenic. If the cord be divided below the point of exit of the phrenics, the connecting channel between the respiratory centre and lungs via the spinal cord is not interfered with, but the resulting paralysis of the abdominal and intercostal muscles necessitates that the action of the diaphragm should be more powerful. If one phrenic nerve be divided, half the diaphragm is paralysed; if both be divided, the whole diaphragm is paralysed, and in most animals death ensues. In the horse division of the phrenic nerves is not fatal; it leads to difficulty in breathing, increased heart action, and the collection of fæces in the rectum; but in about twenty-four hours these symptoms pass away, and if the animal be worked, no appreciable difficulty in breathing is subsequently observed.

We are not prepared to offer any explanation of this remarkable exception to experimental division of both phrenic nerves. Sometimes the fact may be demonstrated in surgical practice, for though as a rule in the horse fracture of any one of the four upper cervical vertebræ, *i.e.*, fracture above the origin of the phrenic nerves, is immediately fatal, yet there are many exceptions to the rule, and death may be delayed for some time.

The phrenic nuclei in the cord are connected by crossed fibres, so that, if the cord be half cut through above the nuclei, both sides of the diaphragm are still able to contract, the explanation being that the impulses cut off from one half of the diaphragm are transmitted through the crossed channel.

Division of Seventh Pair.—Colin has shown that if the seventh pair of nerves be divided in the horse, and the animal worked, asphyxia results. This nerve dilates the nostrils; when it is divided, the paralysed flaccid nostrils are drawn inward at each inspiration, and so close the opening.

Cause of First Inspiration.—The cause of the first act of inspiration in the newly-born animal is that the placental circulation being cut off, the respiratory centre of the fœtus becomes stimulated through the increased venous character of the blood now circulating through it; as a result of this, inspiration is automatically produced. But it is also assisted by reflex impulses carried from the surface of the skin due to handling and drying; handling the skin of the fœtus while still *in utero* with the placental circulation intact may provoke respirations, and in all animals the very first act of the mother is to dry the body of the young and stimulate the skin by licking.

The Amount of Air Required.—Numerous respiration experiments have been made on all animals to determine the amount of air they require and the gases of respiration. It is, perhaps, to a knowledge of the respiration of the horse that the greatest practical interest attaches, although a knowledge of the respiration of other animals is also of value.

The lungs of a horse will contain about 42·5 litres (1½ cubic feet) of air at the end of a deep inspiration. During ordinary repose he draws into them 2,265 to 2,548 litres (between 80 and 90 cubic feet) of air in the hour, though considerable variation may be found even in the same animal.

An average inspiration in the horse during repose amounts to about 4·1 litres (250 cubic inches), and the amount of air which flows in and out during ordinary quiet respiration is known as the *tidal air*. Speaking roughly, it is only one-tenth of what the lungs can contain; the remaining nine-tenths are made up of *complemental, reserve,* and *residual air*. The *complemental* air is that over and above the tidal which can be taken in by a forced inspiration, while the *reserve* is a somewhat similar amount which can be expelled by a forced expiration. The most powerful expiratory effort is unable to remove from the lungs all the air they contain, and this remainder is known as the *residual* air.

The great variations which have been observed in the amount of air taken in by the same animals, under apparently identical conditions, cannot be adequately explained; the slightest disturbing influence alters both the rhythm and depth of the respirations. Under the influence of work, the amount of air required is greater, and as a rule, the faster the pace the more air needed; but many disturbing factors occur which render experiments on this subject very contradictory, and give results of the greatest variation. During severe work, such as a gallop, a horse is taking air into his lungs at the rate of 24,067 litres (850 cubic feet) per hour at least, and probably more; the respirations, from being 9 to 10 per minute during repose, may now be anything between 70 and 100 per minute. The effect of taking in all this extra air is that the *pulmonary ventilation* is increased. It is calculated that in man a deep inspiration more than doubles the capacity of the alveoli by distending them. In such paces as the canter, trot, and walk, the amount of air used is correspondingly less; immediately the pace slackens or the horse stops, the respirations fall, and the amount of air inspired becomes reduced. This is one of the great difficulties attending respiration experiments on horses under natural conditions.

In the following table is shown the mean amount of expired air obtained from horses performing actual work, and collected in the apparatus shown in Figs. 52 and 53:

	Air expired in Litres per Hour.	Air expired in Cubic Feet per Hour.
Repose - - -	2099·75	74·17
Walk - - -	3780·80	133·55
Trot - - -	8149·70	287·87
Canter - - -	11069·21	391·00
Gallop - - -	24038·02	849·10

A horse in a state of repose, according to Zuntz and Lehmann, produces 85 litres (3 cubic feet) of CO_2 per hour, and absorbs nearly 99 litres (3½ cubic feet) of oxygen; the expired air is found to have lost 4 per cent. of its oxygen and gained 3½ per cent. of CO_2. This is very much more than we found,* but it agrees pretty closely with observations made on other animals and on man. It may be noted that even in animals which, from their small size or from other causes, lend themselves to exactitude in experimentation, the most divergent results have been obtained, and the same divergence is observed in experiments in man.

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* 'The Chemistry of Respiration in the Horse during Rest and Work,' *Journal of Physiology*, vol. xi., 1890. It is now considered that samples of air are not sufficient to determine respiratory exchanges; the CO_2 has a tendency to accumulate in the tissues, and an apparatus such as was employed by Zuntz and Lehmann, which admits of prolonged observation, is necessary.

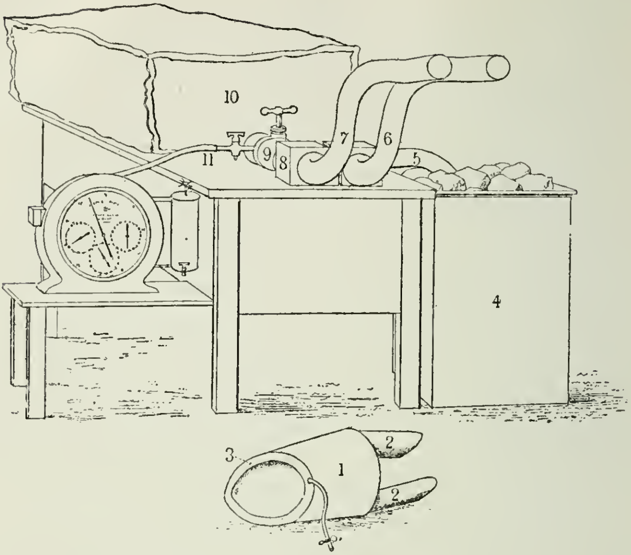

Fig. 52.—Respiration Apparatus.

1, The face mask; 2, rubber connections with 6 and 7; 3, pneumatic collar to render mask air-tight above; 6 is the inlet to the face-piece, and 7 the outlet to the bag; 8, valve-box through which the expired air passes to 10, a rubber bag of 20 cubic feet capacity. After an experiment, the tap 9 is closed and the air pressed out of the bag, passing through 11, where it is measured in the meter. 4, A chamber containing a tray of coke saturated with caustic potash, through which the inspired air passes and is robbed of its CO_2 before entering 5 and 6.

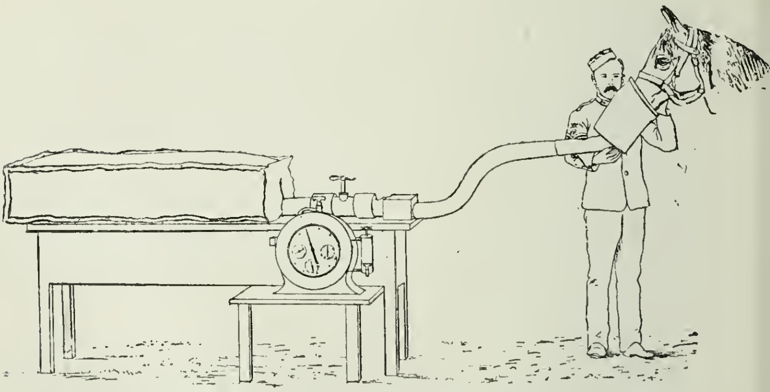

Fig. 53.—Horse in Position on Respiration Apparatus.

Muscular work has a profound influence over the respiratory exchange; it increases the amount of oxygen absorbed and the proportion of carbon dioxide given off. The faster the pace, the greater the amount of exchange which occurs, though experiment has failed to prove definitely an immediate relationship between the amount of oxygen absorbed and the amount of work produced.

The following table is taken from the experiments of Zuntz and Lehmann on horses:*

	Air expired per Hour.		Carbon Dioxide discharged per Hour.		Oxygen absorbed per Hour.		Respiratory Quotient.
	Litres.	Cubic Feet.	Litres.	Cubic Feet.	Litres.	Cubic Feet.	
Rest	2,640	93·2	88·68	3·13	96·06	3·39	0·92
Walk	10,620	375·1	260·52	9·20	285·96	10·10	0·90
Trot	19,980	705·7	450·96	15·90	485·58	17·15	0·93

The table on p. 146 taken from Colin gives a general view of the respiratory changes in animals. It represents the mean of observations made many years ago by different authorities, but Laulanié considers the figures to be too high; they certainly are so far as the horse is concerned, but are of interest from a comparative point of view.

The column showing the respiratory changes per kilo of body weight illustrates the fact, to which attention will subsequently be drawn, that the changes among small animals are greater than among large ones, owing to their having, relatively to their weight, greater body surface. The discharge of carbon dioxide by a mouse, for example, is relatively sixteen or seventeen times greater than that of an ox.

The Influence of Work on Respirations.—During moderate work the increase of carbon dioxide in the alveoli of the lungs is sufficient, as we have seen, to increase the pulmonary ventilation; but with prolonged and especially with severe work it is probable that there are formed in the muscle fibre some products of its metabolism, which may, by circulating through the blood, either stimulate the respiratory centre, or render it still more sensitive to the percentage of carbon dioxide circulating through it.

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* The work performed in these experiments was carried out on a platform revolving at different speeds, and the animal was thus kept in constant communication with the respiratory apparatus, from which samples of the expired air were taken for analysis. It has been shown that this is a necessary condition to insure accuracy. The writer's observations were carried out on horses which actually performed, under natural conditions, the various paces, but the samples of air were unavoidably collected for too brief a period.

	Horse.	Cow.	Ass.	Pig.	Sheep.	Dog.
Body Weight:						
Kilos	450	450	150	75	45	20
Pounds	990	990	330	165	99	44
Amount of air inspired in 24 hours:						
Litres	95,591	78,800	31,495	34,444	20,400	8,441
Cubic feet	3376	2783	1112	1216	720	298
Grammes of oxygen consumed per kilo of body weight in 24 hours	13·272	11·040	13·577	29·698	29·314	28·392
Amount of oxygen consumed in 24 hours:						
Litres	4251·6	3456·0	1417·3	1550·0	918·0	397·86
Cubic feet	150·0	122·0	50·0	54·7	32·4	14·0
Grammes of carbon dioxide produced per kilo of body weight in 24 hours	5·08	4·128	5·08	11·166	7·638	7·621
Amount of carbon dioxide produced in 24 hours:						
Litres	4285·55	3465·75	1427·52	1562·12	641·17	291·76
Cubic feet	151·0	122·3	50·4	55·1	22·6	10·3

The next table is given by Munk:

Animal.	Body Weight.		Oxygen absorbed Daily.		Carbon Dioxide given off Daily.	
	Kilos.	Pounds.	Litres.	Cubic Feet.	Litres.	Cubic Feet.
Horse	450	990	4270·0	150·800	4867	171·90
Ox	600	1320	5565·0	196·500	5548	196·00
Sheep	70	154	605·2	21·377	580	20·48
Dog	15	33	297·5	10·500	224	7·91

Evidence that the panting respirations of work may be due to the presence of a chemical substance circulating in the blood is afforded by the experiment of dividing the spinal cord in the dog, and stimulating the muscles of the hind limbs. The animal, of course, is unconscious of any movement, but the respirations are increased as if it had been running for some distance. What the substance is that gives rise to this is not known. Lactic acid has been suggested, though this is now known to be rapidly oxidised, and dilute acids injected into the blood give rise to much the same condition. Hurried respirations may also be produced through the circulatory system. In an animal in training the breathlessness which it is one of the objects of training to get rid of, is due, not only to the need for oxygen, but also to the fact that more blood is brought to the lungs than can be disposed of. If the right heart pumps into the lungs more blood than the lungs can return to the left heart, breathlessness follows. The gallop by which an animal gets its 'wind' and 'staying' power produces its effects by operating on the circulatory system. Fortunately, the vessels of the lungs are capable of considerable adjustment; they hold more blood during inspiration than expiration, and in this way may be regarded as a safety valve to the heart. The important practical questions of work, 'condition,' and fatigue will be again referred to in the chapter dealing with the Muscular System.

Air vitiated by Respiration was at one time believed to be poisonous, either on account of its deficiency in oxygen, its increase in carbon dioxide, or because of the organic matter mixed up with it. It is now generally admitted that the ill-effects of vitiated air are mainly due to the stagnation of the air and to the warm and humid atmosphere, by which the respiratory exchange and body metabolism are affected. Even the number of bacteria in the air is no criterion of its purity; there may be fewer in expired air than in the same air before inspiration, in consequence of their being arrested in the lungs. Nevertheless, modern inquiry supports the principle contained in the old view, of the evil resulting from breathing atmosphere charged with CO_2. When that gas accumulates to the extent of 4 per cent., rapid breathing and general distress begin to be evident.

The calculation of the amount of air required for effective ventilation is conveniently based on the amount of permissible impurity, as judged by the proportion of carbon dioxide present. Many observations show that when 0·02 per cent. of carbon dioxide is present, in addition to that in the air as a normal impurity—viz., 0·03 per cent.—the ventilation may be regarded as effective. On this basis, if the rate of CO_2 production by any given animal is known, it is easy to calculate the number of times the air of the building should be changed, in order to maintain it in a pure condition.

Respiratory Murmur.—An accurate acquaintance with the normal respiratory murmur is essential to the physician. The air sounds both of inspiration and expiration should be heard all over the chest, the inspiratory murmur being louder and better marked than the expiratory; in fact, in many perfectly healthy chests the expiratory murmur can scarcely be heard. The normal murmur, whether inspiratory or expiratory, is soft in character; there is no harshness. The sound is best represented by the noise made by the stream of air which issues from a pair of hand-bellows when gently blown.

The respiratory murmur, also known as the *vesicular murmur*, is caused by the friction of the air entering the alveoli. Laulanié states that after division of the vagi in the horse all vesicular murmur is lost. In those portions of the lung lying close to the bronchi and larger tubes there is, in addition to the vesicular murmur, a sound produced by the trachea and glottis. This is not distinct from the vesicular sound, but is added to it, the result being that the respiratory murmur over the tubes is louder than elsewhere. The expiratory sound is weaker and shorter than the inspiratory—that is to say, the sound is not continued to the end of expiration, but dies away before that is reached. The expiratory murmur immediately follows the inspiratory without a pause, but there is a marked pause between the end of one expiration and the beginning of the next inspiration.

The ordinary murmur is best heard where the chest wall is thin; if the ribs be covered with fat or any great thickness of muscle, the sound may be entirely lost. It is also important to note that there are some chests perfectly healthy where, for no apparent reason, the respiratory murmur is weak or even undetectable.

SECTION 2.

The Larynx.

The larynx serves a twofold purpose—viz., for respiration and for phonation; in animals the former is the more important, the voice-producing function being of a very subordinate character.

The larynx may be described as a cartilaginous box placed at the summit of the trachea, the opening into it being capable of increasing or decreasing in size, and so of allowing a larger or smaller amount of air to enter the lungs. Within the larynx are two elastic cords arranged in **V** shape, the function of which is solely the production of sound (Fig. 54, 3). Both the respiratory and vocal functions require that the several parts of the larynx should move—viz., that the mouth of the organ should be widened or narrowed, or that the cords should be approximated, drawn apart, tightened, or slackened. These movements are brought about by certain groups of muscles, those which approximate the walls of the glottis being known as the adductors, whilst those which widen it are known as the abductors.

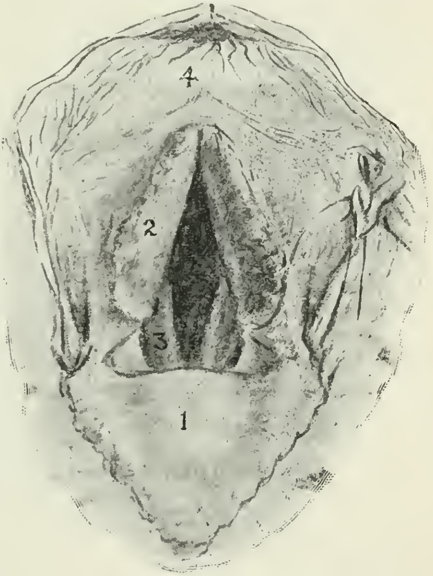

FIG. 54.—THE LARYNGEAL OPENING DURING ORDINARY RESPIRATION.

1, The epiglottis; 2, margin of arytenoids; 3, vocal cord; 4, pharynx laid open. The **V**-shaped slit is the glottis. Note how much wider the epiglottis is than the opening it has to cover.

The **Muscles of the Larynx** may be divided into those of respiration and phonation. As the most important feature in respiration is the opening or dilating of the glottis, the term respiratory muscle might be confined to the dilators of the glottis, while the constrictors would represent the vocal muscles; but the constrictors are not entirely without respiratory function, as, for example, in coughing, so that in the following table they are included under this head:

Respiratory Muscles.

Dilator or abductor,	*Crico-arytenoideus posticus.*
Constrictors or adductors of the glottis,	*Crico-arytenoideus lateralis, Arytenoideus, and Thyro-arytenoideus.*

Phonatory Muscles.

Muscle which relaxes the vocal cords,	*Thyro-arytenoideus,* anterior and especially posterior fasciculus.
Muscle which renders the cords tense,	*Crico-thyroid.*
Muscles which bring the cords together,	The respiratory adductors.
Muscle which moves the cords apart,	The respiratory abductor.

These muscles are shown in Fig. 55.

The crico-arytenoidei, lateralis and posticus, are direct antagonists; the lateralis depresses the arytenoid cartilages and closes the entrance into the glottis, the posticus swings the arytenoids upwards and outwards and enlarges the glottis.

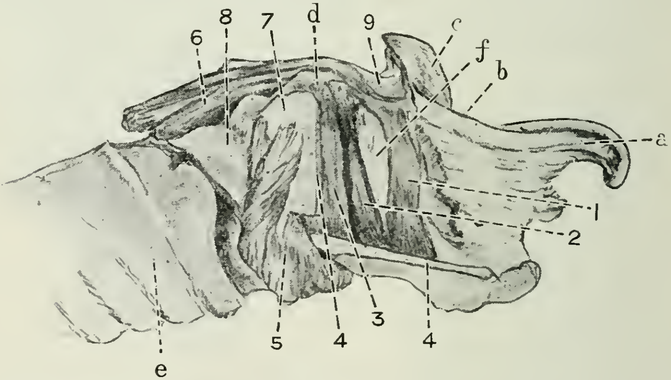

FIG. 55.—THE POSITION OF THE MUSCLES OF THE LARYNX IN THE HORSE.

a, Epiglottis; *b*, opening leading to the glottis; *c*, portion of the arytenoid cartilage; *d*, position of the joint formed between the cricoid and arytenoid cartilages; *e*, the trachea. The wing of the thyroid cartilage has been removed, so as to expose the constrictor muscles; 4, 4, represents its cut edges. 1 and 2, Thyro-arytenoideus: 1, anterior; 2, posterior fascicules. The space *f* between these two muscles indicates the position of the ventricle of the larynx. 3, Crico-arytenoideus lateralis; 5, crico-thyroid muscle, half of which lies inside the thyroid cartilage, and cannot, therefore, be seen; 6, crico-arytenoideus posticus; 7, portion of thyroid cartilage; 8, portion of cricoid cartilage; 9, arytenoideus muscle.

The entrance to the larynx is formed by the two arytenoid cartilages, the epiglottis, and the aryepiglottic folds; beyond these is the glottis proper—viz., the **V**-shaped opening formed by the vocal cords. When the laryngeal opening dilates, the vocal cords pass towards the walls of the cavity and render the **V**-shaped space wider; when the larynx closes, the cords are approximated and the space rendered narrower (Figs. 54 and 56). During ordinary respiration there is very little, if any, alteration in the shape and size of the glottis; but during exertion every inspiratory movement is accompanied by an increase in size, every expiration by a decrease. At each expiration the vocal cords pass towards the centre line, and at each inspiration return to the walls of the larynx. The closure of the larynx, as during the act of swallowing, is a powerful movement, and if the finger at this moment be introduced into the cavity and placed between the arytenoids, it experiences considerable pressure. The closure of the larynx is brought about by the depression and approximation of the arytenoid cartilages and the approximation of the vocal cords; in addition, during the act of swallowing, the base of the tongue presses the epiglottis over the arytenoids and renders the part both air- and water-tight.

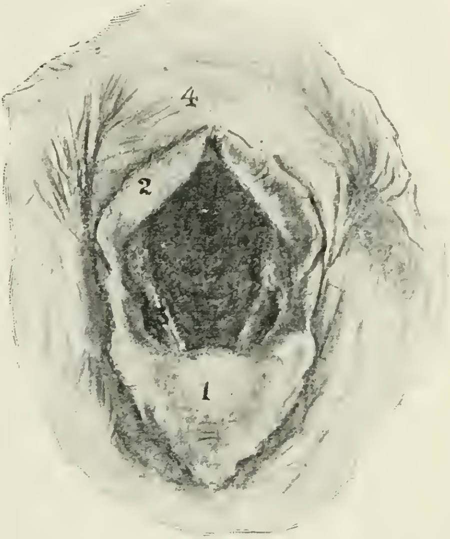

FIG. 56.—THE LARYNGEAL OPENING DURING HURRIED RESPIRATION, SEEN IN A STATE OF DILATATION.

1, Epiglottis; 2, margin of arytenoids; 3, vocal cord; 4, pharynx laid open. Note the size and shape of the glottal opening as compared with the same in Fig. 54.

The **Epiglottis** is much larger than the opening it is intended to seal during a condition of laryngeal repose; it is, as just described, carried, during the act of swallowing, backwards by the base of the tongue and pressed over the arytenoids; the larynx at the same moment advances, with its arytenoid cartilages closely approximated. After the act of swallowing, the tongue advances, the larynx recedes, and the epiglottis returns to its position by means of its elastic recoil. It is not essential to a food- or water-tight condition of the larynx that the epiglottis should exist; it has been removed both by disease and experimentally, and its place is then taken by the base of the tongue. Nor is an arytenoid cartilage essential to safety in swallowing.

The **Nervous Mechanism of the Larynx** is peculiar. In the majority of animals sensation is supplied to the mucous lining membrane, and motor power to the crico-thyroid muscle by the superior laryngeal branch of the vagus, this nerve containing both sensory and motor fibres. In the horse the motor fibres in the superior laryngeal are, it is said, derived from the first cervical nerve and not from the vagus. All the other muscles, both abductor and adductor, are supplied with motor power by the inferior or recurrent laryngeal branch of the vagus. It is strange that both abductor and adductor muscles should have the same source of nerve supply, and one naturally asks what it is which determines that only the opening or only the closing muscles shall act at any given moment? The explanation lies in the law of 'reciprocal innervation,' demonstrated for the limb muscles by Sherrington, which will be considered later in the chapter on the Nervous System. Both dilator and constrictor fibres run in the recurrent laryngeal nerve, and are quite distinct; in some animals the different bundles have been experimentally isolated and injured—injury to the dilator fibres producing abductor paralysis, and injury to the fibres going to the muscles which close the larynx producing adductor paralysis.

If the recurrent laryngeal be cut and the peripheral end strongly stimulated, the glottis almost invariably is found to close; in other words, only the adductor fibres appear to be acted upon. If a *weak* stimulation be applied, the glottis opens—*i.e.*, the abductor muscles are affected.

Another curious fact in the history of the recurrent nerves is furnished by pathology. In the disease of horses known as '**roaring**,' there is paralysis of the left abductor muscle of the larynx—viz., the crico-arytenoideus posticus, the wasting, and fatty degeneration due to paralysis being very marked. It is not unusual to find the adductor muscles normal in appearance, or presenting very little sign of disease, and, even if they are pale and wasted, the degree of degeneration cannot be compared with that of the abductor muscle. This is a difficult fact to explain; one would think that as both abductor and adductor muscles receive the same nerve-supply, equal wasting would occur in both groups. Again, it is observed when the left recurrent has been divided experimentally, that the abductor muscle loses its irritability long before the adductors, and the same fact may be observed in post-mortem stimulation of the nerves. If the recurrent laryngeal nerves be divided under ether, and the peripheral ends stimulated, adduction of the larynx is obtained; but if the ether narcosis be pushed to a dangerous extent and the nerves then stimulated, the glottis dilates—that is, abduction follows. These and other observations have furnished a law which is of clinical significance—viz., that in *functional* disturbance of the larynx the adductor muscles are first affected, but that in changes accompanied by organic lesions the abductor muscles are the first to suffer.

When one recurrent laryngeal nerve is divided, the vocal cord on that side remains immovable and therefore cannot approach its fellow; the healthy cord endeavours to compensate for the weakness of its companion by passing beyond the middle line of the larynx in its attempt to come into contact with it.

The inspiratory distress occasioned in ' roaring ' is not caused, as has been said, by a paralysed vocal cord flapping about, for the elastic nature of the cord, and the fact that the only muscle never affected with paralysis is the one which keeps the vocal cord tense, negative this. The sound is produced by the paralysed left arytenoid cartilage being drawn into the glottis at each inspiration, and this is the explanation why the noise which accompanies the disease is always *inspiratory* and never expiratory. The drawing into the glottal opening of the paralysed arytenoid cartilage is due not only to the inrush of air, but also to the unbalanced action of the antagonists of the dilator muscle.

Phonation.—Voice is produced by the approximation and vibration of the vocal cords, the *pitch* of the voice being produced by the tension of the cords, whilst the *quality* is due to the shape of the cords—viz., their thickness or thinness. The position of the resonant chambers, such as the mouth, pharynx, posterior nares, and even the nasal chambers, also importantly affects the quality of the voice. It is obvious that the chief alterations in the larynx during phonation have reference to the vocal cords; these are approximated by the adductor muscles, and separated by the abductor muscles, whilst they are relaxed by the thyro-arytenoideus and tightened by the crico-thyroid. The latter muscle has a peculiar action; it lowers the thyroid cartilage on to the cricoid and swings the wing of the thyroid outwards, thus rendering the cords tense. These changes in the vocal cords produce changes in the shape of the V-shaped glottal opening; in a high note the glottis is reduced to a mere slit, in deeper notes the cords are separated. If air be forced through the larynx of a dead horse, and the tension of the cords altered, a sound remarkably like a neigh may be produced. The ventricles of the larynx and the cavities of the mouth, nose, pharynx, etc., act as resonators.

Being filled with air, they effect the needful alterations in the quality of the voice, and assist in giving it its distinctive character; thus the false nostrils furnish the 'snort' of the frightened or 'fresh' horse, the nasal chambers the whinny and neigh of pleasure, the mouth and pharynx the neigh of impatience, loneliness, excitement, etc. We do not consider that the guttural pouches act as resonators, and Colin obtained no alteration in the character of the neigh by opening them.

The voice of each species of animal—horse, ass, ox, sheep, and pig—is so distinctive that we may recognise the animal without seeing it; yet though the larynx in all these animals is more or less different, the difference is not sufficient to offer any explanation as to why the sounds emitted are so entirely distinct. The voice of male and female animals differs in intensity. The wild neigh of the stallion is very different from the neigh of the mare, and the bellowing of the bull is distinct from the 'lowing' of the cow. The operation of castration has a remarkable effect on the voice, the neigh of the gelding resembling that of the mare.

In the horse the voice is used during sexual and ordinary excitement, also during fear or especially loneliness, during pain, anger, and as a mark of pleasure. It is not possible to convey in words the difference in the notes produced, but the various sounds are easy to recognise. The horse is essentially a sociable animal; when accustomed to be in the company of others he dislikes separation, and shows it by persistent neighing, which is perhaps more noticeable amongst army horses than amongst any others. The neigh of pleasure is often spoken of as the 'whinny'; the word rather conveys some idea of the sound made. Sounds which can be described only as 'screams' are often evoked during 'horse-play' and temper, or by mares during œstrum. It is not a scream as we know it in the human subject, but no other word conveys an idea of its shrillness. If a horse cries from pain (a very rare occurrence), as during a surgical operation, the cry is a muffled one and short; it is a groan rather than a cry.

In the cerebral cortex voice is represented in the præcrucial and neighbouring gyrus in the dog, and in corresponding regions in other animals. Stimulation of this region leads to *bilateral* adduction of the cords, which suggests that both sides of the larynx are represented in each hemisphere. There is no region in the cortex of the dog which, on stimulation, leads to abduction of the cords, though such a region is found in the cat. It would appear that adduction of the cords is represented in the cortex, as the muscles producing it are especially associated with the production of voice, which is under the influence of the will. Respiration, on the other hand, is automatic, and the abductor muscles being essentially respiratory, their centre is found to exist in the medulla.

Neighing in the horse is produced by an expiration, partly through the nostrils and partly through the mouth; **braying** in the ass is both inspiratory and expiratory, nostrils and mouth each taking a share in it. The ventricles of the larynx are large in the horse and relatively still larger in the ass and mule; they act as resonators and allow of free vibration of the vocal cords. Their obliteration as a surgical treatment for roaring is said to be productive of marked benefit, but this can only be due to cicatricial tissue limiting the movement of the paralysed arytenoid cartilage, for the ventricles take no share in the cause of the disease. According to Chauveau both ass and mule have the subepiglottic sinus provided with a thin membrane capable of vibrating. In the ox, sheep, and goat, the larynx is very simple; there are only rudimentary vocal cords and no ventricles. The **bellowing** of the ox and the **bleating** of the sheep are expiratory efforts through the mouth. The dog and cat have the larynx something like that of the horse, but the ventricles are shallow; the voice is produced almost entirely through the mouth, though both growling and purring may occur through the nostrils.

Castration in early life influences the voice of both geldings and oxen, as the larynx remains imperfectly developed.

Yawning is a deep, slow inspiration followed by a short expiration; the air, even in the horse, is taken in by the mouth, which is widely opened, the jaws being crossed.

Sneezing and **Coughing** are expiratory efforts. The former occurs solely through the nose, and, excepting in the dog and cat, is unaccompanied by the peculiar sound attending this act in the human subject. If snuff be introduced into the nostrils of the horse, a peculiar though well-known vibration of the nostrils occurs as if the animal were blowing its nose, and this is, in fact, what it accomplishes. It is an entirely nasal sound; the mouth takes no part in the act. Coughing occurs through the mouth, the long palate in the horse being raised for the purpose. Before coughing can occur the lungs must be filled with air and the glottis closed; a forcible expiration follows, the glottis opens, and the air is expelled through the mouth.

Hiccough is due to a sudden contraction of the diaphragm. While the air is rushing into the lungs the glottis closes, and the incoming air, striking the closed glottis, produces the sound. The condition known as spasm of the diaphragm in the horse is very different from a human hiccough, and is referred to more fully on p. 156.

Pathological.

Pneumonia and Pleurisy in the horse are very common in early life, and attended by a high mortality. The lungs and pleura, separately or combined, may suffer a degree of inflammation varying from small localised trouble to general and extensive inflammation of the pleura and lungs. The whole of the lung tissue is never affected; even in the most severe cases of pneumonia there is some breathing area available; the upper portion of both lungs generally escapes. Effusion of fluid into the cavity of the thorax is a common sequel to pleurisy in the horse.

Both the above pathological conditions as well as their progress are diagnosed by auscultation and percussion; there are many departures from the normal respiratory murmur, each of which has its significance.

Apoplexy of the Lungs arises as the result of overwork, especially in hot weather; but it may also occur in the winter. Horses ridden to death in the hunting field, in the name of 'sport,' die as a rule from pulmonary apoplexy; the lungs cannot get rid of their abnormal burden of blood to the left heart.

Bronchitis is a disease probably rarely distinct from pneumonia.

'Broken Wind' is one of the most interesting of the various chest diseases of the horse; it is a condition peculiar to this animal, liable to occur suddenly, and frequently traced to errors in dieting. To state the case shortly, *the lungs lose their power of elastic recoil*, and do not collapse even after death; the respirations are greatly increased, the expiratory effort being powerful, characteristically irregular, and prolonged. A chronic typical cough becomes established, and the animal unfit for anything but slow work. On post-mortem examination the lungs are found to fill the chest entirely; they cannot collapse, for all elastic recoil has left them. One of the fundamental errors in veterinary pathology is to attribute this condition to asthma. If healthy lungs be powerfully and repeatedly distended immediately after death, subpleural emphysema is produced or even the pleura ruptured in consequence of the rupture of the air cells; the lungs have largely, though not entirely, lost their power of elastic recoil; in other words, an artificial 'broken wind' has been produced. We must certainly look upon violent and prolonged exertion especially on a full stomach as the chief, if not the sole, cause of the disease.

Roaring is a nervous affection, to which sufficient allusion has been made in the section dealing with the larynx. One point may be emphasised, in consequence of the frequency with which the larynx is now surgically treated, and that is, an injury, however slight, to a cartilage of the larynx is always followed by thickening and ossification, with consequent reduction in the lumen of the larynx. The logical treatment of the disease is to establish a fresh nerve-supply. The writer many years ago demonstrated on the horse that if the left recurrent nerve of a healthy larynx be divided and the distal end sutured to the central end of the spinal accessory, the dilator muscle could be innervated from this new source. A new axis cylinder has to grow through the degenerate nerve, so that the process of restoration is a slow one.

Spasm of the Diaphragm is another respiratory affection due to disordered nervous supply. The sound emitted is quite unlike that in the human subject; it appears to come from within the chest or abdomen, and is represented by a dull 'thud' like a magnified heart-beat, which, in its frequency and regularity, it closely resembles, and for which it may easily be mistaken.

Rupture of the Diaphragm is a common lesion frequently due to disorders of the digestive canal, the gas generated in the intestine being sufficient to burst the diaphragm. Falls are by no means an uncommon cause; for example, an animal falls on to its head, and the abdominal viscera are propelled against the diaphragm. The diaphragm rarely gives way below, almost always above, and in the tendinous substance rather than in the muscular. This point is of physiological interest.

Catarrh.—As the horse can breathe only through the nostrils, obstruction of these passages from catarrh renders the animal unfit for work, even when no other symptoms of importance are present. In the facial sinuses collections of pus are frequent and troublesome.

Laryngitis is frequently the result of strangles infection, rarely of ordinary cold. In the former condition local œdema and dyspnœa are not infrequent, and arise suddenly.

In the ox pneumonia is rare, with the exception of the specially highly infectious type, constituting one of the animal plagues. Practically none of the other diseases mentioned above as affecting the horse are found in any ruminant.

The number and character of the respirations are not only a trustworthy guide during the onset and progress of disease, but their character may be absolutely diagnostic. Broken wind and hydrothorax may be determined by a glance at the flanks; stertorous breathing suggests cerebral compression; while any noise in repose accompanying the inspiratory act in the horse is suggestive of commencing œdema of the pharynx or larynx or nasal passages, as in acute glanders, especially of the mule.

CHAPTER V

DIGESTION

SECTION I.

Digestion in the Mouth.

Prehension of Food.—The methods by which animals convey food to the mouth differ according to the species. In the horse the lips play an important part, for which purpose they are thick, mobile, remarkably strong, and endowed with acute sensation; in the ox they serve a subordinate function, being rigid and wanting in mobility; in the sheep the upper lip is cleft in such a manner as to divide it completely into two parts, each possessing independent movement; in the pig the lower lip is pointed and the upper one insignificant.

A horse, when grazing, advances one fore-leg to enable the mouth to reach the ground; the jugular veins and those of the face distend, and the parotid glands bulge, owing to the enlarged condition of the veins beneath them. With the mouth on the ground the eyes are roughly on a level with the knees, but no animal with the eyes laterally placed is able to see what it is eating; it is guided entirely by the sense of smell.

In manger feeding the horse collects the food with the lips, but in grazing cuts off the grass with the incisor teeth, drawing the lips back in order that he may bite more closely to the ground. In the ox the tongue is protruded and curled round the grass, which is thus drawn into the mouth and taken off between the incisor teeth and the dental pad. In the sheep the divided upper lip allows of the incisors and dental pad biting close to the ground, so that animals of the sheep and goat class can live on land where others such as the horse and ox would starve. In whatever way the food is cut off, it is carried back by the movements of the tongue to the molar teeth, there to undergo a more or less complete grinding.

In the ox and sheep the incisor teeth move freely in their sockets; the object of this is to prevent injury to the dental pad, for which purpose also they are placed very obliquely in the jaw. In the horse the incisor teeth in early life are very upright, but become oblique with age. The molars in all herbivora are compound teeth; in the horse they are very large, especially those in the upper jaw. Being composed of materials of different degrees of hardness, they wear with a rough surface, which is very essential to the grinding and crushing they have to inflict on grasses and grain. The teeth in herbivora, both incisors and molars, are constantly, though slowly, being pushed out of the sockets which hold them; in this way wear and tear is compensated for, whilst the fang of the tooth becomes correspondingly reduced in length. It is owing to this fact that the incisor teeth alter in shape and direction, and so enable the age to be determined. The tables of the molar teeth are not flat, but oblique; this is especially well seen in the horse, where the cutting surface is chisel-shaped, the upper teeth being longest on the outside, while those of the lower row are longest on the inside (see Fig. 57). This arrangement produces sharp teeth, which are a constant source of trouble and loss of condition in horses.

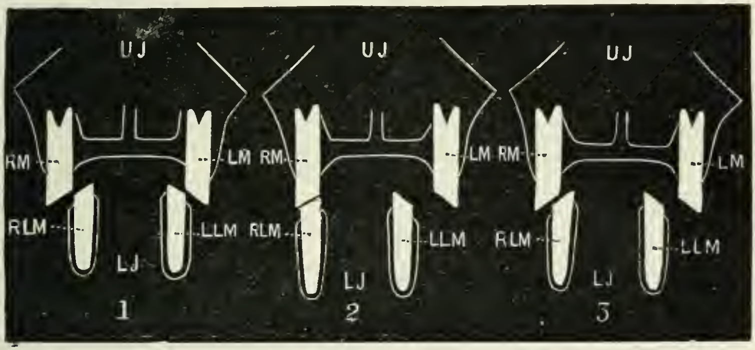

FIG. 57.—SCHEMATIC TRANSVERSE SECTION OF THE UPPER AND LOWER JAWS OF THE HORSE BETWEEN THE THIRD AND FOURTH MOLARS, SHOWING THE POSITION OF THE TABLES OF THE TEETH DURING REST AND MASTICATION.

UJ, Upper jaw; LJ, lower jaw; RM, right molar; LM, left molar; RLM, right lower molar; LLM, left lower molar. 1, The position of the teeth during rest, the outside edge of the lower row in apposition with the inside edge of the upper. 2, The jaws fully crossed masticating from left to right; the tables of both upper and lower molars now rest on each other. 3, The position halfway through the act of mastication, the outer half of the lower teeth wearing against the inner half of the upper.

The movements of the tongue are important. In the ox and dog they are very extensive, the former animal having no difficulty in protruding the tongue and even in introducing the tip into the nostrils. It is not a very common habit in horses to protrude the tongue except when yawning, but they have considerable power in withdrawing it in the mouth. A great difference exists between the tongue of the horse and that of the ox, the former is flabby, broad and flat at the end, constricted opposite the frenum, and swelling out at the apex; it is comparatively smooth on its surface. The tongue of the ox narrows from base to apex, the latter being pointed; it is very rough, which prevents it from losing its hold on the food, protects it from such injury as might be inflicted by coarse grasses, and is also of value to the animal in cleaning its body. The tongue is supplied with motor power by the hypoglossal nerve and with sensation by the lingual branch of the fifth, which supplies the anterior two-thirds of the mucous membrane, the posterior third being supplied by the lingual branch of the glosso-pharyngeal; the same nerve also supplies the sense of taste to this part of the organ, while taste for the anterior two-thirds is supplied by the chorda tympani of the seventh pair. Division of the hypoglossal nerve prevents the ruminant from grazing, the dog from lapping, and in all animals causes the tongue to suffer injury by its being unable to avoid the incisor teeth.

The inside of the mouth of the ox is covered with long papillæ, which point backwards; these would appear to be of use in preventing the food from falling out of the mouth. In the horse no such papillæ exist; in fact, the lining membrane of this part is remarkably smooth. The majority of animals have grooves in the palate; they are well marked in the horse, ox, sheep, and even in the dog. Their function is probably to assist the tongue to pass the food back in the mouth.

Drinking is performed by the animal drawing the tongue backwards, and thus using it as the piston of a suction-pump; this action produces a vacuum in the front of the mouth, as the result of which the cheeks are drawn inwards, the lips at the same time being closed all round, excepting a small space in front which is placed under water. Such is the method in both horse and ox; in the former animal the head is extended while drinking, the ears are drawn forward at each swallow, and during the interval fall back. The cause of this motion is not clear, but is probably due to the movement of air in the guttural pouches. A thirsty horse will swallow from 150 to 250 grammes (5 to 8 ounces) of fluid at each gulp. In drinking off the ground the fluid has to travel against gravity. Lapping in the dog is performed by curling the tongue in such a way as to convert it into a spoon. Sucking, like drinking, is produced by the animal creating a vacuum in the mouth by closing the lips, decreasing the size of the tongue in front and increasing it behind, the dorsum being applied to the roof of the mouth. The foal places the tongue beneath the nipple and curls it in from each side; by this means he protects it from the lower incisors and gets a better hold.

Mastication.

Mastication is performed between the molar teeth; the movements which the jaws undergo, to admit of this being carried out, depend upon the class of animal. In the dog they are very simple, being only a depression and elevation of the jaw; this motion means a simple temporo-maxillary articulation, and such is met with in this animal. In the horse and ox the movement is not only up and down, but lateral, and some say even from front to rear. This necessitates a complex joint capable of affording a considerable amount of play, and this is provided by a disc of cartilage, placed in the articulation, which accommodates the joint to the varying movements required of it in the horse, ox, and sheep, and also saves the part from jar. In herbivora, therefore, we find the cartilage extensively developed, whilst in carnivora it is small and simple. In Fig. 57, 1, the position of the molar teeth at rest is shown; it is obvious that the first act of mastication is to bring the teeth into apposition, and to do this the lower jaw has to be rotated, or, as the expression is, 'crossed' (see Fig. 57, 2). The muscle which effects this rotation is the internal pterygoid, the left muscle pulling the jaw to the right, the right muscle pulling it to the left; meanwhile, in the temporal articulations, the disc of cartilage glides forward on one side and backwards on the other, while the contents of the orbital fossæ are observed in the horse to be alternately ascending and descending. This movement is due to the coronoid process, which pushes up the fossa as the process comes forward and retracts it as the process retires. It is evident that the advancing of the coronoid process, the temporal fossa ascending and the cartilage of the joint gliding forward, are simultaneous actions occurring on that side, right or left, from which the jaw is working, while the retreat of the coronoid process, the descent of the fossa, and the retirement of the cartilage of the joint occur on that side on which the molars are finally brought into apposition. In the hinge-like movement of opening the mouth without mastication occurring both condyles and cartilages come forward.

The temporal joint of the ox is relatively small as compared with that of the horse, and permits of greater lateral movement. In the pig the jaw undergoes very little lateral movement, but extensive protraction and retraction, and the temporal joint is much longer to allow of this. In the dog, hinge-like movement predominates and lateral movement is limited. The herbivora can masticate only on one side at a time; when tired on one side the process is reversed, and the opposite molars take on the crushing. It is surprising how long an animal will carry on mastication on one side; even as long as an hour has been observed in the horse by Colin. This physiologist noticed that in the ox and sheep the first stroke of the molars is in the opposite direction to the regular action which follows; thus, if masticating from right to left the first stroke is made from left to right. It is important to note that in those animals where a single-sided lateral or rotatory movement in mastication is necessary, the upper jaw is always wider than the lower; this we can understand, for if both were the same width the molar teeth would not meet each other when the jaws were crossed for lateral mastication. This extra width of the upper over the lower jaw, in conjunction with the peculiarity of mastication, explains why the molar teeth of the horse and other herbivora wear with sharp chisel edges (see Fig. 57).

When the animal is grazing, very little molar mastication is performed, as the incisors are kept in constant cutting action; cutting and grinding cannot occur simultaneously, but the nature of the food 'at grass' is such that very little mastication is required. The animal remains for long periods with the mouth to the ground, swallowing almost as rapidly as he is cutting off the food, which travels against gravity to the stomach.

Mastication in manger-fed horses is a slow process, though 'greedy' feeders are not unknown. The grinding is very thoroughly performed. The resulting semi-liquid mass weighs from 50 to 100 grammes (1 to 2 ounces), takes about half a minute to produce, and necessitates as a rule about 40 crushings between the molars before being fit for swallowing. This data gives some notion of the amount of work performed by the masseter muscles in eating, say, 2 kilogrammes (4·4 pounds) of hay. Colin, whose results are given above, shows that 5 horses took the following times to eat 2 kilogrammes of hay: 1 hour, 1¼ hours, 1 hour 12 minutes, 1½ hours, 1¾ hours, the last being a very small horse, while the second animal in the series was a big one. The average rate of crushing is 70 to 80 per minute, while the amount of work performed by the jaws working at 420 to 480 times an hour constitutes a distinct source of daily loss. Colin shows that when the animal is very hungry he will prepare and swallow 30 balls in 15 minutes, but as he gets satisfied he does not make more than 10 or 12 swallows in the same time. If the flow of saliva be reduced in amount, the length of time occupied by mastication is naturally increased.

According to the writer's observation, it takes a horse 15 to 20 minutes to eat 1 pound of hay, and 5 to 10 minutes to eat 1 pound of corn.

With the ox the first mastication is imperfectly performed, and is three times quicker than in the horse. When, however, the material is brought back for remastication, the process is slow. In the dog mastication of the natural food, meat, is imperfectly performed; after a few hasty snaps of the jaw the material is swallowed.

Opening the mouth is equivalent to depressing the lower jaw, for the upper takes no share in the process. The muscles which open the mouth are comparatively small, for very little effort is required; the *sterno-* and *stylo-maxillaris* and *digastricus* perform this function. On the other hand, the closing of the jaws in mastication is a difficult task, and for this purpose very powerful muscles exist; they are the *masseters, temporals,* and *pterygoids.* In the dog the temporal muscles are considerably developed, whilst in herbivora the masseters are the largest.

The nerves employed in mastication are the sensory fibres of the fifth, which convey to the brain the impulses resulting from the presence of food in the mouth, while the motor fibres of the same nerve supply the needful stimulus to all the muscles of mastication excepting the *digastricus,* which receives its motor supply from the seventh pair.

Deglutition.

The process of swallowing is usually described as occurring in three stages. The first stage comprises the carrying of the food back to the base of the tongue and pressing it against the soft palate; it is a simple process readily understood. In the second stage the act is complex, for the bolus or fluid has to cross the air-passage, and must be prevented from falling into the nasal chambers, or finding its way down the trachea. To accomplish this in the horse the soft palate is raised and so closes the nasal chambers, the tongue at the same time being carried backwards, while the larynx and pharynx are advanced. This movement causes the base of the tongue to press on the epiglottis and close the larynx, which is further secured by the arytenoid cartilages and vocal cords coming close together. The bolus, liberally coated with mucus from the large mucous crypts in this locality, or the fluid, can now safely pass towards the pharynx, being grasped by the pharyngeal muscles and pressed into the œsophagus. In the third act of swallowing the food is carried down the œsophagus by a continuous wave of contraction, which starts at the pharynx and ends at the stomach. Chauveau points out that, owing to its extreme length, the soft palate of the horse passes completely into the pharynx during the second act of deglutition. The length of the soft palate in this animal prevents food or water being returned by the mouth when once they have entered the pharynx, so that in vomiting, or in cases of sore throat, the food, water, or other material is returned by the nostrils.

It is now considered that in some animals the constrictor muscles of the pharynx take less share in the process of swallowing than was at one time supposed, and that the sharp contraction of the mylo-hyoid muscles of the tongue, together with a backward movement of the organ, exerts pressure on the bolus, and shoots the latter through the pharynx into the œsophagus. From the time the mylo-hyoids act until the entrance of the food into the œsophagus, only a second passes. We are not inclined to think these observations can at present be applied to swallowing in the horse. If the hand is placed in the pharynx there is no suggestion of any such shooting movement, and material, such as a bolus, placed far back on the tongue, is frequently very deliberate in entering the œsophagus. Arloing proved that the passage of fluid along the œsophagus was not due to muscular contractions of that tube, but to the pharyngeal muscles pumping it along the œsophagus. As a matter of fact, fluid scarcely requires one second to reach the stomach, so that its velocity is, as we shall presently see, ten times greater than the rate of œsophageal contraction.

The action of the epiglottis in the closure of the glottis has been much discussed. In the horse it is forced over the opening by the base of the tongue and the advancing larynx; but the epiglottis is not essential to swallowing, for an animal can swallow when it has been removed, and even when one of the arytenoid cartilages has been excised. Placing the finger in the larynx will easily demonstrate that the part closes tightly and forcibly during the second stage of swallowing, the vocal cords and arytenoids being brought so close together that the glottis is perfectly air-tight. It has been pointed out that animals usually swallow with a flexed neck, as in this position the epiglottis is behind the soft palate, and in the most favourable position to be applied over the glottis. It has also been shown, however, that when the head is extended the epiglottis is in the mouth—viz., anterior to the soft palate. We have found it in this position in the horse, and judging from the fact that in a state of nature the horse and ox swallow with an extended and not with a flexed neck, it is probable that in feeding off the ground the epiglottis is anterior to the soft palate. During the third stage of deglutition the bolus can be seen slowly travelling down the channel of the neck; if liquid, however, be passing, the movement is very rapid, for as many as sixty swallows may be made in a minute. As previously noticed, both in eating and drinking the third act of deglutition can occur against gravity; this is because it is a muscular act. The whole process of deglutition is considerably assisted by the salivary secretion. When this has been experimentally diverted, swallowing occurs only with difficulty and very slowly.

The œsophagus of the horse is found to differ considerably from that of most other animals. It is composed for the greater part of its length of red striated muscle, while at and near its termination the previously thin muscular coat becomes very thick and rigid, and the red gives way to pale, non-striped muscle; further, the lumen of the tube becomes very narrow. The thick terminal end of the œsophagus of the horse is always closely contracted, so that if the œsophagus is cut through close to the stomach no material can escape from this organ; this is one explanation why horses vomit with such difficulty. In the ox, sheep, and dog, the tube is composed of red muscle throughout; it terminates in a dilated end at the stomach, and, owing to its thin, distensible walls, even bulky material can pass along it; what the ox and dog can swallow with ease would certainly 'choke' the horse.

Chauveau showed that in the horse the peristaltic contractions of the œsophagus originate in the pharynx, and that, once started, they continue irresistibly to the stomach. A bolus introduced into the œsophagus by a fistula in the neck remains *in situ*; it must start from the pharynx. If by means of a fistula the bolus is discharged externally, the wave of contraction in the œsophagus continues. If the bolus be experimentally arrested, the muscular wave leaves it behind and continues on its journey.

Arloing ascertained the rate of progress of a bolus in the œsophagus of the horse, and found it to be 0·2 metre ($7\frac{3}{4}$ inches) per second in the red portion of the tube and 0·05 metre (1·96 inches) per second in the pale portion. This is evidence that the bolus slows down considerably before it enters the stomach. This observer found the mean time of transit through the œsophagus to be ten seconds. The wave of contraction in the œsophagus is helped by the immediately preceding contraction of the longitudinal muscle, which thereby shortens, and so tends to dilate the tube for the reception of the bolus.

The first stage of deglutition is voluntary, but the remaining processes are quite involuntary, and are brought about by the stimulation of a centre in the medulla known as the swallowing centre. By means of ingoing or afferent nerves supplied by branches of the fifth and by the superior laryngeal, the centre is made acquainted with the fact that food is present in the fauces. A reflex act is now set up in the centre, and an impulse conveyed by outgoing or efferent nerves, furnished by the pharyngeal plexus (composed of the vagus and glosso-pharyngeal) for the constrictor muscles of the pharynx, by the hypoglossal for the tongue, and by the recurrent laryngeal for the muscles which close the glottis. The glosso-pharyngeal is the inhibitory nerve of deglutition; if the central end be stimulated it is impossible to produce the act of swallowing. Further, it is the nerve which immediately inhibits respiration during swallowing, no matter at what phase of the act—viz., inspiration or expiration—the stimulus is applied. Swallowing may be induced without the presence of food in the fauces; touching the rim of the glottis will produce it; so also will pouring a fine jet of fluid into the trachea, or even touching the interior of the trachea as far down as the bronchi.

Stimulation of the mucous membrane of the pharynx excites reflex movements of the œsophagus, but stimulation of the mucous membrane of the œsophagus itself is ineffective in this respect.

The swallowing centre also presides over the œsophagus, and the peristaltic wave from the pharynx to the stomach is produced by impulses sent out from this centre through the vagus. This wave is, therefore, not due to the nerve handing on a contraction by direct conduction from one layer of the muscular wall of the œsophagus to the next. Hence, when once started, it is not arrested either by ligaturing or dividing the œsophagus, though section of the œsophageal nerves prevents it. The contraction wave which sweeps along the œsophagus is not interfered with even by excising a portion of the tube; the wave, having reached the point from which the upper segment has been cut out, appears in due course at the point from which the lower end was removed.

It is not uncommon in watching a bolus pass down the neck of the horse to see it suddenly come to a standstill, and then slowly pass on again after, probably, an attempt to ascend. This is generally due to absence of saliva. In rumination and in vomiting the wave runs upward from the stomach to the pharynx. Division of the vagus interferes with the passage of food along the œsophagus, which in consequence becomes blocked.

The Saliva.

During the process of mastication the food becomes mixed in the mouth with a fluid known as saliva, the secretion of which occurs in three distinct pairs of glands. The method by which it is formed is important to understand, as much the same process occurs in other secretory glands which we have not the same opportunity of watching during their activity.

Classification of Salivary Glands.—The three glands which secrete saliva are the parotid, submaxillary, and sublingual;

these are structurally divided into two groups, mucous and serous (or albuminous) glands, the submaxillary and sublingual being types of the first, the parotid the type of the second.

The following table from Colin shows the relative percentages of the glands in various animals:

	Horse.	Ox.	Sheep.	Pig.	Dog.
Parotid - -	78·00	45·00	52·00	81·00	48·00
Submaxillary -	17·00	48·00	43·00	16·00	52·00
Sublingual - -	00·05	00·07	00·05	00·03	—

The table shows that, excepting the pig, the horse has the best-developed parotid system, while his submaxillary glands are very small. In the ox the parotid and submaxillary glands are nearly equal in weight. Colin showed that the size of a salivary gland does not determine its secretory power; the parotid of the horse secretes from fifteen to twenty times more saliva than the submaxillary, while it is only about five times heavier. Similarly, the parotid of the ox secretes four times more saliva than the submaxillary, though they are of nearly equal weight.

All the salivary glands belong to the class known as 'compound tubular.' The parotid is regarded as the type of serous (or albuminous) gland, and this holds good in all animals; but the submaxillary is sometimes of the mucous type, as in the dog and cat, and sometimes mixed, as in man. The sublingual may also be a mixed gland, though with mucous cells predominating.

Mucous glands are generally characterised by the presence of peculiar crescent-shaped cells known as *demilunes*, lying beneath the basement membrane, and away from the central lumen of the tube. Great difference of opinion has existed as to the special function of these *crescents of Gianuzzi*, some believing that they replace worn-out mucous cells, others that they possess specific functions.

It has been supposed that the activity of the three glands depends upon the character of the food substances, and in the dog there is experimental proof of the correctness of this view. Pavlov, whose work on digestion has opened up a new field, has shown that in the dog—and the following remarks refer solely to this animal—the submaxillary gland responds to the sight of food, to the chewing of meat, and to the action of acids; while the parotid responds to dry food, such as dry powdered meat, bread, or biscuit.

The selective power of the glands and their adaptability to the class of food in the mouth is very remarkable. Dry bread excites the parotid, since water is required to moisten it, and the submaxillary, since mucin is needed in order to lubricate it, but moist bread stimulates only the submaxillary. Fresh meat requires no parotid, but only submaxillary saliva. Pebbles placed in the mouth excite little or no secretion, but pebbles reduced to sand excite an abundant secretion. It has been suggested that this abundant secretion is to wash out the sand, while pebbles require no washing out, as they can be dropped. What is still more remarkable, it has been shown that the *sight* of food causes an abundant secretion of saliva; Claude Bernard demonstrated that this was also true of the horse.

From this it is evident that no stimulation of the buccal mucous membrane is essential to secretion, though there can be little doubt that the adaptative mechanism is frequently provoked through this channel.

Colin in opposition to Bernard stated that in the herbivora the secretion of saliva was uninfluenced by the sight or smell of food; nor could he obtain any secretion from the parotids by the employment of excitants to the mucous membrane of the mouth; salts, acids, aromatic substances, all gave equally negative results in this respect. The submaxillary and sublingual glands, on the other hand, actively responded to these stimuli. In the horse he found that oats produced a greater secretion of saliva than hay, though the amount of fluid absorbed by oats is one-quarter that by hay.

It is well known that fear or anxiety gives rise in the human subject to impulses inhibiting secretion of saliva; the mouth becomes dry, and the tongue refuses to move. In the horse an identical condition is produced by abdominal pain. During an attack of colic the mouth is quite dry, which symptom is of the utmost value. The dryness is not due to thirst, for the animal never drinks while the pain lasts; a moist condition of mouth and a desire for water are two favourable indications of the utmost value in prognosis.

Physical and Chemical Characters.—Mixed saliva is an alkaline, opalescent, or slightly turbid fluid which readily froths when shaken. On standing exposed to the air, it throws down a deposit of carbonate of lime due to the loss of its carbonic acid. It has a specific gravity of 1·005 in the horse, and 1·010 in the ox. Examined microscopically, saliva is seen to contain epithelial scales and salivary corpuscles. The latter are small round granular cells which seem to be altered leucocytes, and are probably derived from the soft palate. About 0·6 per cent. of the saliva consists of mineral matter, and 0·2 per cent., more or less, of organic matter, the latter consisting of mucin (which gives saliva its well-known viscidity and ropiness), and small amounts of protein substances the nature of which has not been exactly determined. Mucin belongs to a peculiar group of protein bodies combined with a carbohydrate, for which see Chapter XX. Ptyalin or salivary diastase is the most interesting organic constituent of saliva in man, and belongs to a group of ferments known as unorganised. It is doubtful if it exists in the herbivora, and under no circumstances has its amount been determined. Ptyalin is also absent from the saliva of the dog. The salts of saliva are principally carbonate of lime, alkaline chlorides, and phosphates of lime and magnesia. Sulpho-cyanates are found in minute quantities in the saliva of the human subject, but are absent from that of the horse. The gases of the saliva are principally carbonic acid, with traces of oxygen and nitrogen; there is no body fluid which contains so much carbonic acid as saliva (65 volumes per cent.). The three salivas have different physical properties. Parotid saliva is watery, clear, and free from mucin, but contains a small quantity of protein; submaxillary and sublingual salivas are viscid, especially the latter, owing to their richness in mucin. The watery saliva has to impregnate the food and prepare it for digestion, but the viscid salivas are concerned principally in swallowing.

Amount of Secretion.—Colin observed some remarkable facts regarding the secretion of the various salivary glands in the herbivora. When an animal is masticating, the parotid on that side is secreting, while its fellow is almost at rest. When the rhythm of mastication changes over to the opposite side, the parotid on that side becomes active, while the other passes into the condition of comparative rest. The parotid of the side on which the animal is masticating will secrete two, three, or four times as much saliva as its fellow. The following table shows one of Colin's experiments on the horse:

	Right Parotid.	Left Parotid.	Direction of Mastication.
	Grammes.	Grammes.	
3 minutes	50	110	To the left
6 ,,	200	50	To the right
4 ,,	30	100	To the left
5 ,,	200	30	To the right

So far, these observations apply both to the horse and to the ruminant, but differences soon occur. When the horse is no longer eating, the parotids stop secreting, but with the ruminant this is not the case; the parotids continue to act, not only during rumination, but during abstinence. During rumination the secretion is unilateral in the sense that very much more is obtained from the side on which the jaws are active.

The secretion from the submaxillary and sublingual glands behaves quite differently from that of the parotid. It is constant from both sides in all herbivora, no matter what the direction of mastication may be. The submaxillary glands cease to secrete during rumination; the sublingual is not affected by this function.

The actual amount of fluid secreted daily from these glands in the large herbivora is astonishing. Colin put it down at 5 to 6 kilogrammes (8½ to 10½ pints) hourly for the horse during the seven hours he is engaged in feeding. He gives the total daily secretion for this animal at 42 kilogrammes (9¼ gallons), while for the ox it is still higher—56 kilogrammes (12¼ gallons), of which from 800 grammes (1·4 pints) to 2,400 grammes (4¼ pints) per hour are produced during the intervals of feeding.

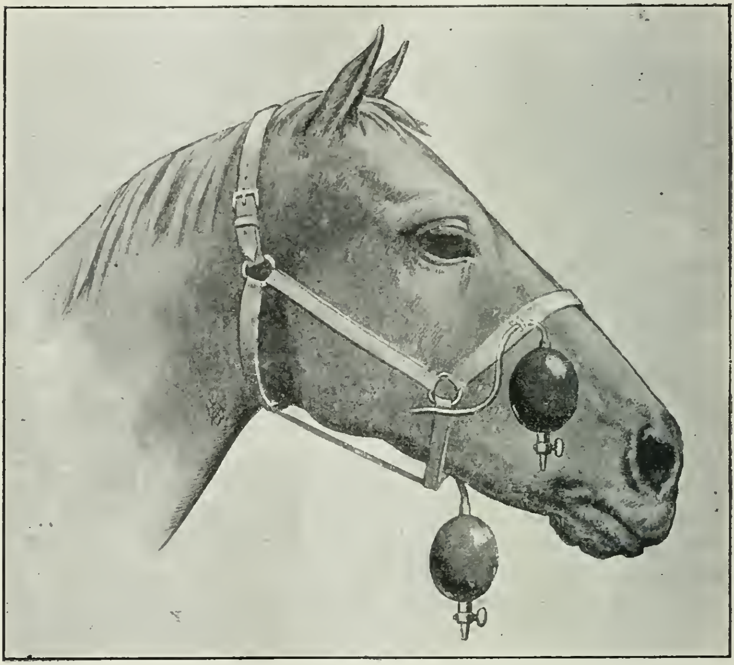

FIG. 58.—APPARATUS EMPLOYED BY COLIN IN EXPERIMENTS ON THE SECRETION OF PAROTID AND SUBMAXILLARY SALIVA.

The submaxillary secretion is placed at 280 grammes (1½ pints) per hour, and the sublingual at 18 to 20 grammes (¾ ounce) per hour.

It is obvious that the amount of secretion depends upon the character of the food· only half the daily mean is secreted if green food be given, and only one-third if roots form the diet. On the other hand, oats increase the amount secreted. Hay absorbs four times its own weight of saliva, oats a little more than their weight, and green fodder half its weight.

The **use of the saliva** in herbivora is to assist in mastication and swallowing, in stimulating the nerves of taste, and in ruminants to assist in rumination. According to the writer's observations on the horse, confirmed by R. J. Seymour in 1917 and C. E. Hayden in 1918,* saliva has no chemical action on the raw starch of the food, and this is not surprising when we remember that the starch grains are enclosed in an envelope of cellulose, a substance on which saliva has no action. So intimately, however, is salivary secretion associated with starch conversion, that it is not possible to pass over without further notice the action produced on starch in man, and, according to some observers, in horses and cattle, by the presence of ptyalin in the saliva.

The starch found in plants exists in the form of granules which are of shapes peculiar to the various species; these granules are enveloped in tough envelopes of cellulose; before the true starch, the *granulose* contained in the cellulose envelope, can be reached the cellulose must be traversed. For this reason some animals, like man, cannot digest raw starch, but by being cooked the starch (granulose) is liberated and made free to be acted upon; on the other hand, all the herbivora are capable of digesting raw starch, perhaps because they can digest cellulose.

If boiled starch be mixed with filtered human saliva and kept at a temperature of 95° F., in a short time the characteristic reaction of a blue colour with iodine disappears on the addition of this reagent, and a reddish colour is formed, indicating the presence of a substance known as **erythrodextrin**. The fluid, which before was sugar-free, contains distinct evidence of the presence of this substance; by continuing the action of the saliva it is shortly found that the red colour on the addition of iodine has disappeared, and the fluid gives evidence of containing a considerable proportion of sugar. But analysis shows that for the amount of starch employed the full amount of sugar has not been obtained; in other words, there is a second substance present besides sugar, which is produced as the result of the action of the saliva, and to this the name **achroodextrin** has been given; it is formed from the erythrodextrin. The sugar formed from starch by the action of saliva is not grape-sugar, but maltose; glucose (dextrose or grape-sugar) being found only in small quantities, if at all. This action of the saliva on starch is described as the **Amylolytic** action; it is due to the presence of ptyalin.

* *American Journal of Physiology.*

Ptyalin, the active principle of starch-converting salivas, is an unorganised enzyme, and, like all ferments, is of unknown chemical nature. It is capable of converting cooked starch rapidly and raw starch slowly into maltose and dextrin, the ferment acting by hydrolysis—*i.e.*, the molecule of starch takes up water, and undergoes cleavage into simpler bodies. Between starch and maltose there are doubtless many other bodies, but the chemistry is not agreed upon. The amylolytic action is permanently destroyed by a high, inhibited by a low temperature, retarded by a slightly acid or alkaline medium, and destroyed by free hydrochloric acid. If starch be boiled with a dilute acid, conversion into sugar occurs. The difference between the action of boiling acid on starch and of saliva is that the latter can produce only maltose, whereas the acid produces dextrose.

The view we hold as to the non-amylolytic action of the saliva of the horse is not supported by other observers; Ellenberger* distinctly states that both the parotid and submaxillary secretions of the horse and ox can convert starch into sugar, but in the case of the horse it is only the saliva first secreted by the glands after a rest which possesses this property; as secretion proceeds the power is nearly lost. In the pig, according to this observer, all the salivary glands are starch-converting; in the rabbit the submaxillary has no action, while the parotid is energetic; in the cat, dog, horse, sheep, and ox the action is very feeble or entirely absent. Meade Smith† states that the saliva of the horse will convert crushed raw starch into sugar in fifteen minutes, and that the process begun in the mouth is continued in the stomach; he further adds that the saliva of the horse will convert cane into grape sugar.

The amylolytic properties of equine saliva have been inquired into recently by Lieut.-Colonel Watkins Pitchford, C.M.G., R.A.V.C., at the Central Veterinary Research Laboratory at Aldershot. A washed sponge inserted into the mouth of the horse becomes rapidly saturated with the salivary secretion, which is readily collected in this manner in considerable quantities.

Observation with the saliva thus obtained from a series of ten horses showed in all cases the presence of an amylolytic ferment existent both before and after feeding. In these experiments the starch was either partly converted into maltose and erythrodextrin or completely into maltose, Fehling's test showing the presence of sugar in abundance in all cases. This amylolytic action was noted to be less marked than in the case of human saliva, but it was evident in dilutions of one part of saliva to five parts of boiled starch solution, within a time limit of thirty minutes at 37° C. With raw oat starch the action is much slower and less complete. (Communicated.)

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* 'Physiologie der Haussäugethiere.'

† 'Physiology of the Domestic Animals.'

In man starch conversion, brought about by the action of ptyalin, is now recognised as taking place in the stomach from the swallowed saliva—in fact, the bulk of the conversion must necessarily take place there, and not in the mouth. There is an abundance of sugar in the stomach of the horse, which the writer suggests is probably formed by a ferment pre-existing in the grain. Pitchford's observations show that with some horses it may originate from the saliva swallowed.

Secretion of Saliva.—The mechanism concerned in the secretion of saliva deserves careful attention, for the reason that it throws considerable light on other secretory processes. The subject has been worked out by so many competent observers that the leading points are beyond all doubt. The submaxillary gland of the dog has mainly afforded the desired information, and there is reason to believe that the same process of secretion holds good for the parotid and other glands, both of this animal and of herbivora.

The chief point in the secretion of saliva is that it is controlled by the nervous system, and is not directly dependent upon any mere increase in the blood-pressure in the gland. Afferent nerves—viz., the gustatory division of the fifth and the glosso-pharyngeal—convey from the mouth to the medulla a certain impulse, which, by means of efferent nerves, is conveyed to the gland, and secretion results. The efferent nerve of the submaxillary gland of the dog is supplied by the **chorda tympani**, a small branch given off by the seventh cranial nerve, which enters the gland at its hilum, and supplies the vessels with dilator and the cells with secretory fibres. The second nerve supplying the submaxillary gland is a branch of the **sympathetic**, which spreads out and invests with constrictor fibres the walls of the artery supplying the part (Fig. 59). Thus the chorda tympani supplies the gland with secretory fibres and the walls of the vessels with dilator fibres, while the sympathetic supplies the vessels with constrictor fibres, and only a few secretory fibres.

If the tongue or the lingual branch of the fifth or glosso-pharyngeal nerves be stimulated, secretion of saliva results; if the sympathetic nerve be divided and the tongue then stimulated, secretion follows; but if the chorda tympani be previously divided, no secretion follows on stimulation of the tongue, lingual, or glosso-pharyngeal nerves. If the chorda be stimulated, the vessels dilate, the gland becomes red, the blood flowing from the veins is arterial in tint, and the veins pulsate; in addition to this, there is an abundant secretion of watery saliva poor in solids.

When the sympathetic is stimulated, exactly the reverse is observed—viz., the vessels constrict, in consequence of which the gland becomes pale, only a small quantity of extremely viscid saliva flows, which is rich in solids, the blood in the veins becomes very dark in colour, and the blood-stream slows to such an extent that if the veins leading from the gland be cut, the flow from them is less than from a gland at rest. That the increased flow of blood to the gland produced by stimulating the chorda is not the essential cause of the secretion is proved by the fact that the pressure of the saliva in the duct of the gland is higher than the blood-pressure within the vessels. Further, if before stimu-

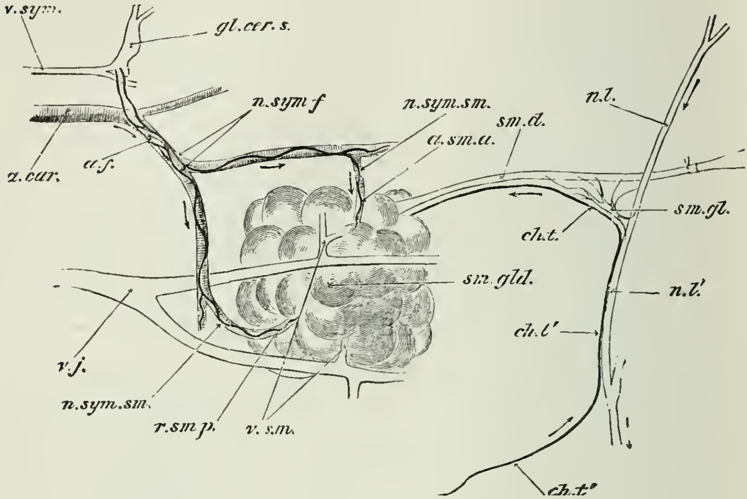

FIG. 59.—DIAGRAMMATIC REPRESENTATION OF THE SUBMAXILLARY GLAND OF THE DOG, WITH ITS NERVES AND BLOODVESSELS (FOSTER).

(The dissection has been made with the animal on its back, and is very diagrammatic).

The submaxillary gland (*sm.gld.*) occupies the centre of the figure; the bloodvessels supplying it, derived from the carotid artery, *a.car.*, are seen on the left, whilst the duct from the gland *sm.d.*, in which a cannula is inserted, is on the right of the figure.

The chorda tympani nerve, *ch.t''.*, running in company with the lingual branch of the fifth *n.l'.*, is seen to the right and below; after running together the two nerves separate, the chorda tympani, *ch.t.*, running along the submaxillary duct to the gland. Close to where the two nerves separate is the submaxillary ganglion, *sm.gl.*

The sympathetic nerve-supply is shown in the figure to the left and above, the fibres being derived from the superior cervical ganglion, *gl.cer.s.*, and coursing along the bloodvessels to enter the gland.

The bloodvessels leading from the gland fall into the jugular vein, *v.j.*

The arrows indicate the direction of the nervous impulses during the reflex act, ascending to the brain by the lingual, and descending by the chorda.

lation of the chorda some *atropine* be injected, stimulation of the nerve still produces to the full all the vascular changes, but not a trace of saliva is secreted. Hence, secretion is not due merely to increased blood-pressure. This atropine experiment proves the existence in the chorda of two sets of nerves—viz., secretory and vaso-dilator; owing to the action of atropine, the secretory nerves are paralysed, while the vaso-dilators are not. In the sympathetic two sets of nerves can similarly be demonstrated—secretory and vaso-constrictor—though it is most likely that in the majority of animals the secretory fibres in the sympathetic are few in number. *Pilocarpine* is antagonistic to atropine, and produces a profuse flow of saliva.

A peculiar phenomenon is observed in connection with salivary secretion after division of the chorda. Though the gland is cut off from its secretory nerve, yet one or two days after section a secretion appears, and may continue for some weeks until the gland undergoes atrophy. This is known as 'paralytic secretion.' The cause of paralytic secretion is not definitely known. The cut portion of nerve in connection with the gland degenerates; it has been suggested that the secreting cells are controlled by inhibitory fibres in the nerve, and that the cells, in consequence of a local nervous mechanism in the gland, continue secreting. Very little of a definite nature is known of the paralytic phenomenon, and it is curious to observe that it is not limited to the gland of which the nerve has been divided, but affects both sides. Langley, who has described this, refers to the continuous secretion from the unoperated gland as *antiparalytic* or *antilytic*.

Heidenhain's view of the action of secretory nerves is that a gland is supplied with a trophic or nutritive nerve which excites the formation of the organic constituents of the secretion, and a secretory nerve, which controls the secretion of water and inorganic salts. The cranial nerves are chiefly secretory, while the sympathetic are trophic, or building up; hence stimulation of the chorda yields the water and salts of the saliva, while stimulation of the sympathetic produces the organic substances and ferment.

Trophic fibres are supposed to effect a breaking-down of the complex living substance of the gland and conversion into simpler bodies, and that chemical changes of importance are occurring is undoubted from the large amount of CO_2 found in saliva, which indicates active oxidation. Saliva contains more CO_2 than any other secretion of the body—more, even, than venous blood. Side by side with the above destructive changes construction must also be going on, though there are no known nerve fibres responsible for the process. As to the manner in which the secretory nerves act very little is known; the blood loses more water than can be accounted for by the amount in the saliva, the difference being supposed to be represented by an increase in the lymph flow from the fluid; but in what way nerve impulses can cause the cells to secrete is at present inexplicable.

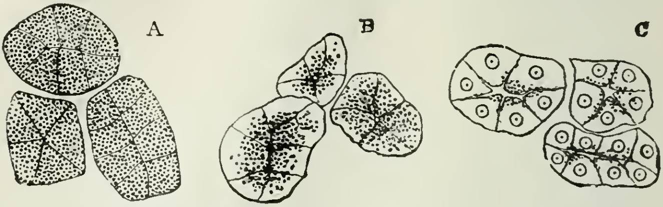

Fig. 60.—Changes in the Cells of the Living Parotid (Serous Gland) during Secretion (Foster, after Langley).

A, At rest; B, in the first stage of secretion; C, after prolonged secretion.

The method by which secretion in the parotid gland is carried out differs in no essential respect from that in the submaxillary. The nerves supplying the parotid are the glosso-pharyngeal (the action of which corresponds to the chorda of the submaxillary) and the sympathetic. In the glosso-pharyngeal are dilator fibres, and in the sympathetic constrictor fibres for the blood-vessels, while both trunks contain secretory nerves.

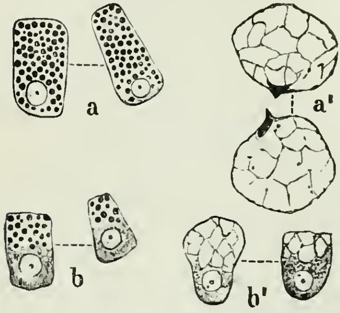

Fig. 61.—Cells from Mucous Gland (Submaxillary Gland of the Dog) (Foster).

a, From loaded gland; b, from discharged gland; a′, b′, treated with dilute acetic acid; a′, from loaded; b′, from discharged gland.

The influence of atropine and pilocarpine on the gland-cells has previously been mentioned; it remains to notice the effect of *nicotine,* which prevents the secretion of saliva—not, however, by its action on the gland-cells, but by paralysing the connections of the nerve fibres in such ganglia as the submaxillary, Langley's, and the superior cervical. This action of nicotine, which essentially consists in paralysing the *nerve-cells* in the ganglia, and not the fibres, was discovered by Langley, and has largely helped in building up our knowledge of the sympathetic system.

The changes occurring in the cells of the salivary glands during secretion depend upon the type of gland. We select Langley's observations, since he examined the living gland, and not one simply hardened and stained. During the stage of rest in a living serous gland, such as the parotid, the cells are found to be filled with a quantity of granular material, and the outline of each individual cell is indistinct; the lumen of the gland is also occluded, and no nucleus can be observed in the cells; in other words, the gland is charged with its secretory products (Fig. 60, A). During activity the cells get rid of their granular material, which gradually passes towards the centre of the acinus or lumen, leaving each cell with a clear outer edge, while that edge next the lumen is still granular (Fig. 60, B). In an exhausted condition the cells are smaller and remarkably clear, only a few granules being left in them on the inner edge, while the lumen is now distinct and large, and the nuclei are clearly seen occupying a central position (Fig. 60, C).

If a mucous gland, such as the submaxillary, be examined at rest under like conditions, the cells are found filled with granules much larger than those of a serous gland, and a nucleus is seen occupying one edge of the cell (Fig. 61, a). During activity the granules are passed into the lumen of the gland, but they do not leave behind them in the cells the same clear space seen in the serous cell (Fig. 61, b). If the cells, while in an active condition, be acted upon by water or dilute acetic acid, the granules swell up and become transparent owing to the mucin they contain, and a delicate network is seen to pervade the cell (Fig. 61, a′). A similar appearance is produced in the exhausted cell (Fig. 61, b′), excepting that less transparent mucin is seen and more granular substance, while the nucleus of the exhausted irrigated gland is seen passing towards the centre of the cell instead of remaining close to the outer wall. Though we have spoken of these granules as mucin, in the gland they are not really mucin, but the mother-substance of it—viz., *mucigen*—which during the act of secretion is converted into mucin. The same holds good for the serous type; the granules in the resting gland are the precursors of the ferment or the *zymogen* of the secretion, from which the secretion is actually formed at the moment it is poured out.

The outcome of the changes above described proves that the organic elements found in the salivary secretion are manufactured by the cells in the glands; the inorganic constituents are either the result of filtration or of secretion. Experiments made by Langley and Fletcher go to prove that even water and salts are the result of cell secretion, and not of mere transudation.

SECTION 2.

Stomach Digestion.

Important digestive changes in the food of the lower animals take place in the stomach. It is not a matter for surprise to find that the size and shape of this organ varies with the species of animal; we should expect a simple stomach in the dog, and complex arrangement in vegetable feeders. It seems remarkable that any animal should possess a laboratory capable of converting grass, hay, and grain into muscle and fat; and it is evident that the conversion of vegetable into animal tissues must be a more complex process than the conversion of animal tissues into the living structure of an animal body. But it is curious to observe that a complex stomach is by no means a necessity for a vegetable feeder; the stomach of the ruminant and the simple stomach of the horse could not be in greater contrast, while the laboratory processes of digestion are practically identical. So far as vegetable food is concerned, it does not matter whether the solution and absorption of its readily soluble matters comes before maceration, or whether maceration precedes the extraction of the readily soluble substances. If maceration comes first, as in ruminants, bulky gastric compartments are provided for the purpose, and the subsequent intestinal canal is short. If the simple stomach comes first, bulky intestines for the purpose of maceration follow; in both cases ample provision is made in the stomach for the maceration necessary for the solution of the cell-wall and fibrous portion of plants. The dog, with its simple stomach and simple intestines, offers no difficulty to our understanding. He lives on flesh, and converts it into flesh; it is not very clear why he has both a stomach and intestines, for the whole process of digestion is simple, and could be readily carried out by the intestines alone. In fact, the stomach of the dog has been removed experimentally, and the animal remained in health.

For simplicity in construction the stomach of the dog occupies one end of the scale, for complexity the gastric reservoirs of the ox occupy the other, while between the two comes the stomach of the omnivorous pig, partaking of some of the characteristics of the carnivora and of some of the ruminant, and belonging to neither.

Stomach Digestion in the Horse.

The subject of stomach digestion in the horse has been worked out by means of feeding experiments, as it has been found impossible to establish a gastric fistula in this animal owing to the distance of the stomach from the abdominal wall; pure gastric juice has, therefore, never been obtained from the horse.

The first peculiarity to be noticed in soliped digestion is that the stomach is rarely empty; it is only when horses have purposely been deprived of food for not less than twenty-four hours that an empty stomach can be obtained. On the other hand, feeding experiments show that very shortly after food arrives in the stomach it commences to pass out, and the difficulty thus presented to the observer in reconciling these opposed facts is at first sight considerable. It is perfectly true that food does pass out early, it is equally true that it is long retained, these opposite conditions being the result of the periods of digestion. When food enters an empty stomach it passes towards the pylorus, where it meets with a fluid of an alkaline or neutral reaction which has come from the mouth. As more food is consumed an acid fluid is secreted in the stomach, and material commences to pass out at the pylorus into the bowel, the amount passing out not equalling at present the amount passing in. Thus the stomach becomes gradually distended, and when two-thirds full, which is the condition in which the most active digestion occurs, the amount passing out will, if more food be taken, equal the amount being swallowed, so that we have a stream of partly peptonised chyme streaming out of the right extremity, while a corresponding bulk of ingesta is entering the inert left sac. In fact, the stomach may during feeding allow two or three times the bulk of food to pass out which remains in it when the meal is finished. No sooner is the feed finished than the passage of chyme into the duodenum ceases, or becomes so slowed down that only small quantities of food pass out, and so gradual is this passing out that it will be many hours before the stomach is really empty, though, had the process continued as it commenced, the stomach would not have contained anything at the end of an hour. This condition of stomach digestion in the horse may be variously modified, according to the nature of the food, the quantity given, the form in which it is given, the order in which one food follows another, and whether water be given before or after feeding. All these are points requiring our attention, but first we must briefly look at the stomach itself.

The mean capacity of a horse's stomach is, according to Colin, from 15 to 18 litres (3 to 4 gallons); these figures were obtained from a very large number of observations, and give the extreme size of the organ when distended. The viscus is under the best physiological conditions for digestion when it contains about 10 to 12 litres (2 to 2·5 gallons), or is distended to two-thirds of its capacity. The mucous membrane of the stomach of the horse is peculiar; one portion of it, practically half, is a continuation of the membrane of the œsophagus; this ends abruptly, and is succeeded by the villous coat, which extends to the pylorus. It is in this latter coat that a true digestive juice is secreted, though not from the entire surface, for on examination of the villous membrane it is found to show great variations in appearance, the fundus being channelled, furrowed, and velvety, whilst the pyloric portion is smooth. It is in the fundus only that true gastric juice—viz., pepsin and acid—is secreted; in the smooth pyloric mucous membrane pepsin only is formed. The area of the secreting fundus surface is about 1 square foot. Fig. 62 shows the relative positions of the various parts of the mucous membrane of the stomach of the horse; the drawing accurately indicates the shape of the stomach, the positions of the inlet and outlet, and the directions and positions of the various areas. In Fig. 63, after Ellenberger and Baum, is indicated the position of the organ in the living animal.

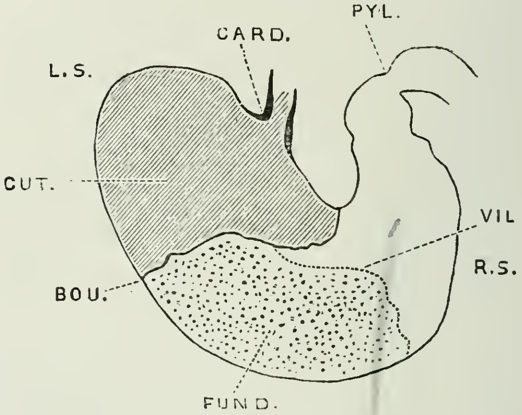

FIG. 62.—LONGITUDINAL SECTION OF THE STOMACH OF THE HORSE.

CARD., Cardia; PYL., pylorus; L.S., left sac; R.S., right sac; CUT., cuticular coat; VIL., villous coat; BOU., boundary-line between the cuticular and villous portions; FUND., fundus of the stomach. The dotted surface indicates the area for the secretion of gastric juice.

There is a want of agreement in the matter of stomach nomenclature. The human physiologist describes the fundus of the stomach as being close to the cardia, whereas we have spoken of it as being at the bottom or on the floor of the stomach, as if it were in the position the name 'fundus' would assign it.* In Fig. 64 are shown the parts of the human stomach according to modern nomenclature. To the left of the figure is seen the

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* The fundus of an organ is the rounded base of a viscus ending in a neck, and having an aperture. It is the bottom of anything.

antrum pylori, marked off by a fissure, IA, and a transverse band for the main body of the organ. The main body is divided into fundus and prepyloric region; it will be observed that the position assigned to the fundus of the human stomach is not that found in the horse. On the other hand, the antrum pylori of the horse is as well marked as in the human subject, possessing both the transverse band and the sacculated condition towards the duodenum.

A very remarkable amount of mucin is secreted by the villous sac of the stomach, and forms over the inner surface of the viscus a thick gelatinous, firmly adherent coating like white of egg, which cannot be washed away even by a powerful jet of water.

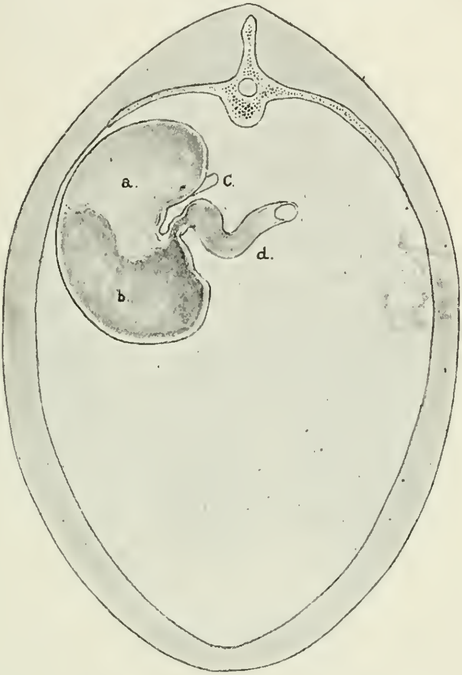


Fig. 63.—Position of the Stomach of the Horse in the Living Animal (after Ellenberger and Baum).

a, Vertical transverse section of the frozen body made through the fourteenth dorsal vertebra, showing the position occupied by the stomach; *c*, œsophagus; *d*, duodenum; *a*, cuticular area; *b*, villous area. As a perfectly vertical section would not give a complete picture of the stomach, owing to its obliquity, the above has been schematically amended. The observer is looking towards the animal's head.

The pyloric orifice of the stomach is usually large and open, and there is a distinct pyloric ring; behind this the duodenum is dilated, and the gut comports itself in such a singular manner (which has a very important bearing on the pathology of the organ) that mention must be made of it here. From the pylorus the duodenum curves down and then up again, forming the letter **U**; so much does this remind one of a well-known form of trap used in drainage that we have described it as the syphon trap of the duodenum (Fig. 65). The use of this trap appears to be to regulate the passage of material from the stomach into the intestines. The writer's observations have shown that its presence in all probability influences rupture of the stomach, for the more distended the large bowels become, the greater the pressure exercised on the duodenum, and in cases of severe tympany the passage from the stomach to the intestines is completely cut off. Should fermentation still continue in the stomach, the contents can neither escape into the œsophagus nor into the bowel, and the coats of the viscus may be completely ruptured under the intense strain. Fig. 63 demonstrates the position the greater curvature of the stomach occupies towards the left ribs. There is no space left into which the stomach can swell. It is held back by the diaphragm, pushed forward by the intestines, bound down by the ribs, and rupture of the greater curvature follows. It was mentioned on p. 165 that the œsophagus of the horse near its termination changes from red to pale muscle, and for several inches increases enormously in thickness. It is this thickened

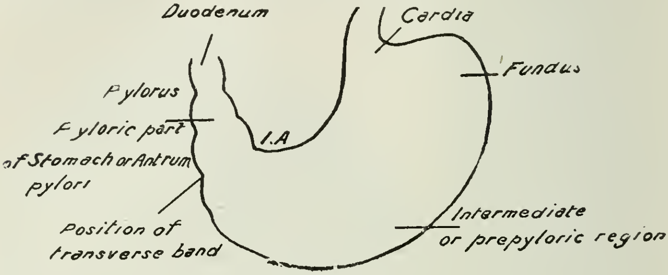

Duodenum
Cardia
Fundus
Pylorus
Pyloric part of Stomach or Antrum pylori
I.A
Position of transverse band
Intermediate or prepyloric region

Fig. 64.—Schematic Figure of the Human Stomach (Howell, after Retzius).

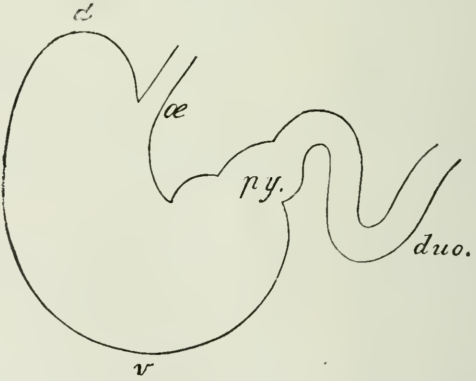


Fig. 65.—Longitudinal Section of the Stomach of the Horse, showing the Syphon Trap of the Duodenum.

œ, Œsophagus; *py.*, pylorus; *d*, left sac; *v*, fundus; *duo.*, duodenum.

contracted end of the œsophagus which completely seals the stomach anteriorly; nothing can be forced out by this passage, not even after death or under great pressure.

The physiological points of interest in the structure of the horse's stomach are: (1) That it is small; (2) that it is not in contact with the abdominal wall, but rests on the colon; (3) that the outlet and inlet are situated close together; (4) that the cardia is tightly constricted; (5) that only a portion of its surface is capable of secreting a digestive fluid; (6) that there are remarkable differences in the character and nature of the various regions of its mucous membrane.

We can now consider the stomach digestion of the two chief foods used for horses—viz., hay and oats.

Digestion of Hay.—Hay, as has been stated, mixes in the mouth with four times its bulk of saliva, and after a very perfect grinding passes into the stomach. If the stomach be empty it is of no size, and the material lies in the lesser curvature and pyloric region; as the viscus gradually fills, the greater curvature is occupied, the gastric juice begins to act, and chyme commences to pass into the intestines probably in a very imperfectly elaborated form. Let us assume the animal to have finished eating hay; we find the output into the intestine now becomes small and slow. The gastric juice has an opportunity of acting more thoroughly upon the ingesta, which turn yellow on that surface which is in contact with the villous wall, the compression of the stomach on the contents causing them to become distinctly moulded into a mass the shape of the viscus. Owing to gravity there is more fluid towards the pylorus than elsewhere, and for the same reason the greater curvature in all probability is fuller than the lesser. The material in the stomach is perfectly comminuted, resembles firm green and yellow fæces, and the smell is peculiar, like that of sour tobacco. The yellowness is due to the gastric juice, and is consequently more marked towards the pylorus; the portion coloured green is the part as yet unacted upon by the juice. The entire surface of the stomach and its contents are now acid, excepting at the cardia, where they may occasionally be alkaline from swallowed saliva; the acidity is greater at the fundus than at the cardia. This general acidity shows that a diffusion of the gastric juice must have been going on. There is no evidence of any churning motion; the cake-like condition into which the hay is compressed is produced by the simple compression of the stomach walls.

The duration of hay-digestion in the stomach is very variable. In examining a series of digestions hour by hour, such as will be mentioned presently, moderately uniform results may be obtained, but even these are sure to be here and there broken by excessive, or conversely by very small, digestions which cannot be explained.

No one can say with any degree of certainty how much hay a horse will digest in any given period, as may be seen from the following observations:

	Amount digested per Cent.
After 4¾ hours' digestion - - - - -	17
" 5 " " - - - - -	66
" 5½ " " - - - - -	64
" 6 " " - - - - -	44
" 9 " " - - - - -	58

It is known, however, that as a rule more will be digested in the first hour, less in the next, still less in the third, and so on until the stomach empties itself, or until what remains in the stomach is actually pushed out by the arrival of the next feed. Assuming, however, that the animal is purposely starved, the stomach may not empty itself for fifteen, eighteen, twenty-four, or even thirty-six hours. It is impossible to say, either at the end of twelve or of thirty-six hours, that the stomach has passed the whole of its contents into the intestine. The writer has found hay in the stomach fifteen and eighteen hours after being given, and under identical experimental conditions the stomach at the fifteenth hour has been found empty.

Colin's elaborate researches furnish very complete data on the question of hay digestion in the horse. In one experiment carried out on fourteen animals he divided them into two groups, each horse receiving 2·5 kilogrammes (5·5 pounds) hay. One group had long, the other chaffed hay. The following table shows the percentage digested at each period:

	Long Hay.	Chaffed Hay.
	Per Cent.	Per Cent.
Amount digested at second hour	61	56
" " third hour -	69	77
" " fourth hour -	73	64
" " fifth hour -	78	91
" " sixth hour -	74	83
" " seventh hour	73	79
" " eighth hour -	88	81

This shows that the rate of digestion falls off after the second hour, so that even at the end of eight hours there is still food left in the stomach. Only one animal digested as much as 90 per cent., and this was at the fifth hour. With this exception the results are fairly uniform, and they further demonstrate that chaffing hay does not increase its rate of digestion.

The influence of water on the digestion of hay was tested by Colin. The following table shows the results, and also furnishes detailed information, hour by hour, of the rate of stomach digestion:

Duration of Digestion.	Hay without drinking Water (per Cent. digested).	Duration of Digestion.	Hay with drinking Water (per Cent. digested).
Hours.		Hours.	
½	30	1½	41 (mean of 2 experiments)
1	45	2	46 ,, 4 ,,
2	37 (mean of 4 experiments)	3	61 ,, 2 ,,
3	52	4	64 ,, 5 ,,
5	77	5	88 ,, 3 ,,
6	66	6	79 ,, 3 ,,
7	64	7	87
8	72	9	82 ,, 2 ,,
10	83	10	92 ,, 2 ,,
11	95	11	95
12	95	12	85 ,, 2 ,,
14	96	13	92
18	96	14	94
		15	97
		16	98

On the whole, during the earlier hours of digestion the horses receiving water digested hay better than those kept without it, but there is no difference after the ninth or tenth hour succeeding feeding.

Digestion of Oats.—Oats take up their own weight of saliva, and during digestion behave much as does hay—viz., while the animal is feeding the contents of the stomach begin very early to pass into the intestine, but the rate is considerably reduced the moment no more material arrives in the organ.

Colin fed six horses on 2·5 kilogrammes (5·5 pounds) oats; three horses received uncrushed, three crushed corn, and the following table shows the percentage digested:

Duration of Digestion.	Crushed Corn (per Cent. digested).	Uncrushed Corn (per Cent. digested).
2 hours - - -	48	45
4 ,, - - -	56	61
6 ,, - - -	62	54

The crushing of the corn made no difference to the rate of digestion—a point of practical importance in dietetics. Comparing this table with the one on p. 184, it would appear that hay is easier of digestion than oats.

The digestion of oats in individual horses is just as irregular as that of hay. A horse to which only 2 pounds of oats were given was destroyed twenty hours later, and the stomach was not completely empty. In another to which 1 pound had been given 6 ounces were recovered after four hours' digestion. In the following table the results of some experimental feedings are recorded:

	Amount digested per Cent.
3 hours	45·0
3 ,,	57·0
3 ,,	70·0
3 ,,	78·6

These horses were fed under similar conditions, yet there is a good deal of variation in the amounts digested. In the next table the period of observation was increased in order to see whether greater uniformity would result:

	Amount digested per Cent.
4 hours	Nil
4 ,,	18·0
4 ,,	54·5
4 ,,	56·0
4 ,,	75·0

These results are less regular than those of the first series; one horse digested nothing, and that is explained by a practical fact capable of being turned to clinical account. The animal was of a very nervous disposition, and the experiment was carried out in a strange stable, the mare being alone, whereas she was used to the company of other animals. The second horse in this series digested only 18 per cent.; this also illustrates a practical point in feeding—namely, the influence of a sudden change in diet. This animal had not received oats for eighteen months, having been fed on a patent food; the sudden change to oats for the experimental observation explains why only 18 per cent. was digested.

Arrangement of Food in the Stomach.—If a horse be fed on oats, maize, hay, etc., in succession, the stomach, on examination, will be found to contain these substances quite unmixed, and arranged in strata in the order of their arrival, the first food being in the pylorus and greater curvature, the last in the cardia and lesser curvature. We have pointed out that the contents of the stomach of the horse are squeezed and pressed, but never churned. In successive feeding one material never mixes with another, excepting at the pylorus, but keeps together from the time of its arrival until it passes out of the stomach, a sharp line of demarcation distinguishing it from its neighbour. If the stomach be empty or greatly contracted, the first food to arrive is lodged in the lesser curvature and pylorus; gradually, as new material arrives, this passes over to the greater curvature in order to make room for itself. If a horse be fed with hay, followed by oats, the presence of the oats causes the hay to pass out more rapidly than it would have done had it been given alone.

Ellenberger has shown that when hay and oats are given in the order named, a portion of the oats may pass into the bowel by the lesser curvature without entering either the left sac or fundus of the stomach (see Fig. 66, I.). When oats followed by hay are given, the oats, as the first arrival, naturally commence to pass out first, but the presence of the hay hurries the rate of progress, and the oats pass more quickly into the intestines than they otherwise would do. The regular arrangement of food in layers is disturbed when a horse is watered after feeding; half the food may in this way be washed out of the stomach, for the water which a horse drinks does not stop in the stomach, but passes directly through it on its way to the cæcum. Hence we have the golden rule of experience that horses should be *watered first and fed afterwards.*

These facts may be summarised by saying that in a succession of foods the first consumed is the first to pass out. That is not to say that the whole of it passes out before any portion of the succeeding food enters the bowel, for we have shown that after a time, at the pylorus, they mix and pass out together; but the actual influence of giving a food first is to cause it to pass out first. The practical application of this fact, according to Ellenberger, is that when foods are given in succession, the least albuminous should be given first. This appears distinctly to reverse the English practice of giving oats first and hay afterwards, but perhaps only apparently so, for experiment shows that the longer digestion is prolonged, the more oats and the less hay pass out, so that some hay (under ordinary circumstances a moderate quantity) is always left in the stomach until the commencement of the next meal. The presence of this hay from the previous feed may prevent the corn of the succeeding meal from passing out too early. According to Ellenberger, in order that horses may obtain the fullest possible nutriment from their oats, hay should be given first, *and then water;* this carries some of the hay into the bowel, and after a time the oats are given. The remaining hay now passes into the bowel, and the oats remain in the stomach. This does not accord with English views of watering and feeding fast-working horses, views which have stood the test of prolonged practical experience.

The appearance of the food after it has been in the stomach depends upon the period of digestion. We have previously drawn attention to the fact that an hour or two after hay has been taken the material is found in a finely-chopped condition, firm—one may almost say dry—in places, though towards the pylorus it is liquid. This hay contains between four and five parts of saliva; it is yellow in colour where the gastric juice has

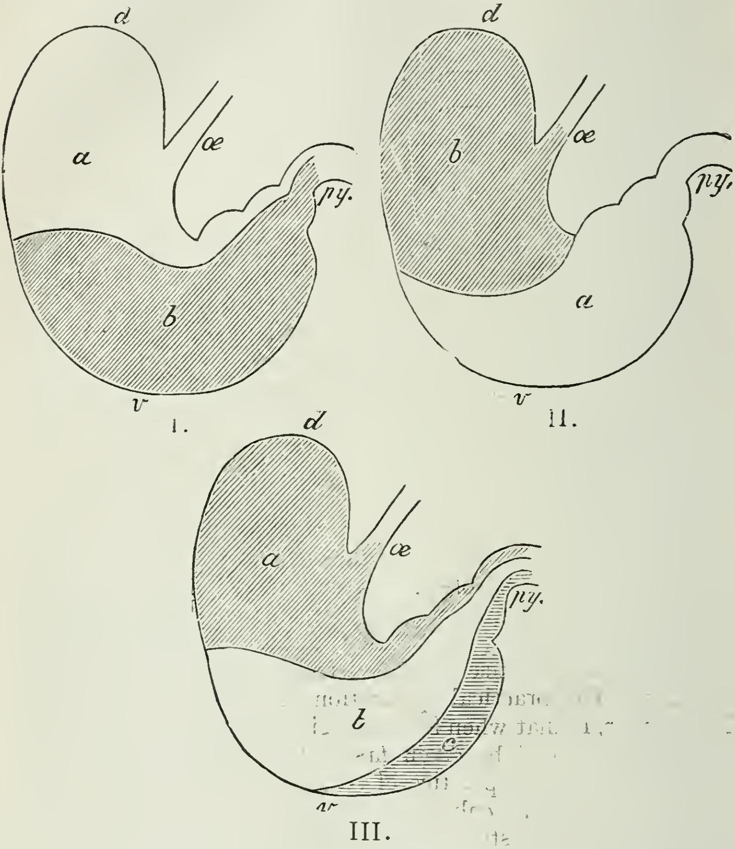


Fig. 66.—Longitudinal Section of the Horse's Stomach, showing the Arrangement of the Food according to the Order in which it was received (Ellenberger).

In each case *œ* is the œsophagus; *py.*, pylorus; *d*, the left sac; *v*, the fundus. I. Hay first, followed by oats: *b*, the hay; *a*, the oats; the latter are passing along the lesser curvature and escaping with the hay at the pylorus. II. Oats first, followed by hay: *a*, the oats; *b*, the hay. III. The order of three successive feeds: *c*, the first feed; *b*, the second; *a*, the third.

attacked it, but of rather a greenish tint elsewhere, and it has a peculiar odour. Several hours after feeding, the stomach is found to contain a variable quantity of watery fluid discoloured by the hay which is left behind, part of which may be found floating on the fluid. At other times, when the stomach is empty, the fluid is viscid, contains numerous gas bubbles, and is of an amber or yellow tint; this particular fluid is no doubt saliva and mucin, with possibly a little bile, the result of a reflux from the bowel. When oats alone have been given, the contents of the stomach are found to be liquid, the fluid being creamy in consistency and colour; the oats are swollen, soft, with the interior exposed; towards the end of digestion the creamy fluid is replaced by the frothy yellow one. With both hay and oats, and also other foods, there is a peculiar sour-milk-like smell from the contents of the stomach, more marked with bran and oats than with hay, the latter, as previously mentioned, smelling like sour tobacco.

The **reaction of the contents of the stomach** is strongly acid; ✓ this acid reaction may be obtained on the cuticular as well as on the villous portion of the lining, and is very persistent; the cuticular membrane, even after prolonged washing, gives an acid reaction. The acidity is derived entirely from the juice secreted by the villous membrane of the fundus. Our observations on this subject do not agree with those of Ellenberger, who says that during the first hour of digestion the contents of the stomach may be alkaline; acidity, he states, then commences in the fundus and extends to the cardia, though for some time the fundus acidity is three or four times greater than that of the cardia; in the course of five or six hours the proportion of acid throughout the stomach is equal. When the stomach is empty, as after a few days' starvation, its reaction is neutral or alkaline. We have observed extreme alkalinity towards the pylorus under these conditions, due, no doubt, to the regurgitation of bile and pancreatic fluid.

Alkalinity of the contents may be met with at the cardiac end of the stomach; in such cases it is due to the swallowed saliva, and the stomach contents at this part exhibit a marked sugar reaction. It is difficult to say whether this alkalinity is invariable; in the writer's experience it has seldom been met with; but the stage of digestion may explain it, for it is easy to understand that during the early period of digestion the stomach acids will not have penetrated to the upper part of the stomach, and in this way have neutralised the immense quantity of salivated food of an alkaline reaction which is swallowed.

The Stomach Acids.—It is not necessary here to enter into any detail as to the nature of the gastric acids; a considerable amount has been written to prove that the acidity, both in the horse and man, depends upon lactic or upon hydrochloric acid, and it is possible that both these views may be reconciled. Ellenberger and Hofmeister are of opinion that shortly after a meal lactic acid predominates in the horse's stomach, to be replaced by hydrochloric acid some four or five hours after the commencement of feeding. These observers found that the nature of the acid depended upon the region of the stomach, the length of digestion, and the character of the food; oats induced an outpouring of hydrochloric acid, whilst hay favoured the organic acids.

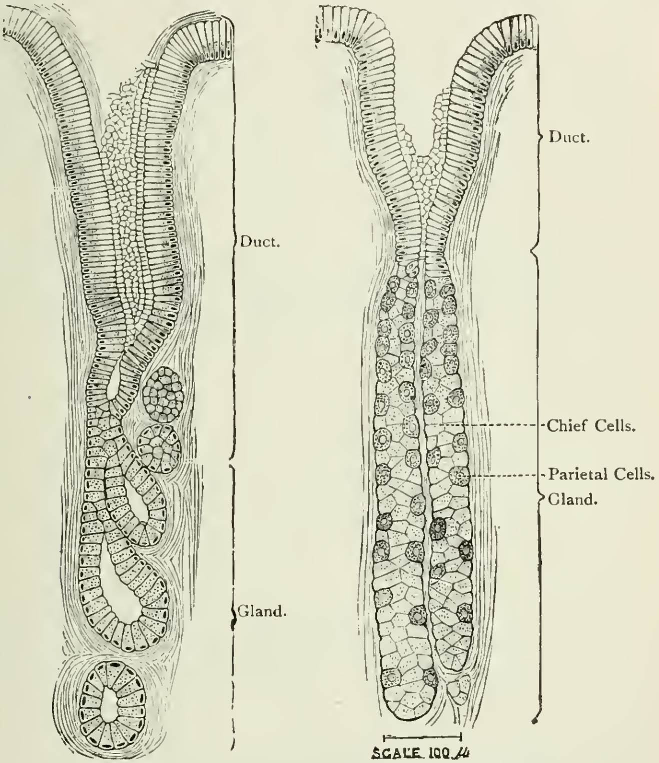
The following are Ellenberger's views on the nature of the stomach acids: in the contents of the stomach, hydrochloric, lactic, butyric, and acetic acids may be found, the two latter in insignificant quantities only. In flesh-feeders HCl predominates, and lactic acid is found in small quantities. In vegetable feeders lactic acid at first predominates, and later HCl is present in small quantities; lactic acid exists throughout the whole stomach, but predominates in the right and left sacs, whilst hydrochloric acid principally exists in the fundus region. Lactic is the first digestive acid employed, but towards the end of a long digestion hydrochloric exists throughout the whole stomach. The amount of lactic acid found in the stomach of the horse during the first hours of digestion is considerable.

It has been suggested that the presence of lactic acid in the stomach of herbivora may be due to the fermentation of the carbohydrates of the food, and this cannot be rejected as a contributory cause. In the dog, in which animal the acid is doubtless hydrochloric, it is well known that no free HCl may be obtained for the first hour or two of digestion, owing to the acid combining with the protein of the food, and to the diminution it undergoes in neutralising the alkali of the saliva.

The writer's experience regarding the presence of hydrochloric acid and organic acids in the stomach contents is that, no matter at what period of digestion observations have been made, on only two or three occasions has he succeeded in finding hydrochloric acid in the stomach of the horse, and he is convinced that lactic is the chief, if not the sole, digestive acid in this animal.

The **Secretion of Gastric Juice** is accomplished in certain glands known as the gastric. In man these are divided into cardiac and pyloric, each having not only a different structure, but a separate function. In the horse cardiac glands are impossible owing to the presence of the cuticular coat; but it has been shown that the villous coat contains glands corresponding to cardiac, which are principally situated in the greater curvature, at the fundus of the stomach, and extend over a limited area.

described on p. 180 as not larger than 1 square foot (Fig. 62). The two kinds of gland employed in the production of gastric juice are both found in the villous coat, the one in the fundus, the other in the pyloric portion, though Ellenberger states that he has found fundus glands in the pyloric region. They are simple or divided tubes lying side by side, and opening, generally in groups, on the surface of the mucous membrane by means of a shallow depression in the coat. These depressions can readily be seen studded over the tunic of the fundus, giving it a rough appearance owing to the elevation of the mucous membrane between the openings of the glands; in the pyloric region the membrane is as smooth as that found in the intestine. Each gland consists of a body, neck, and mouth, and is lined with cells; it is in respect of the cellular contents that the pyloric and fundus glands differ.



PYLORIC GLAND. CARDIAC OR FUNDUS GLAND.

FIG. 67.—THE GASTRIC GLANDS AFTER HEIDENHAIN (WALLER).

The cells of the **fundus gland** (Fig. 67) are small, polyhedral, granular, and nucleated, and line the lumen of the gland; they are called the *principal, central,* or *chief cells.* Scattered amongst the principal cells, but existing in larger numbers at the neck of the gland than at its base, are found certain large cells (oval, granular, and nucleated), which from their position relative to the lumen of the gland are called *parietal, marginal,* or *border cells.* These cells are distinctive of the fundus glands, and they stain readily with aniline blue.

The **pyloric gland** (Fig. 67) below its neck has but one variety of cell—viz., the cylindrical—containing a nucleus at its attached edge. The duct is lined, above the neck, by the ordinary epithelium of the stomach, and the same remark applies to the fundus glands; it is from this epithelium that the mucus is secreted. The important distinction between the fundus gland with principal and parietal cells, and the pyloric gland with principal cells only, is that the former, since the acid is separated from the blood by parietal cells, whilst pepsin only is formed by principal cells, secretes both the pepsin and the acid of the gastric juice, whereas the pyloric glands, made up of principal cells, secrete only pepsin.

We have previously mentioned that the cells of the salivary glands undergo certain changes in appearance, as the results of rest and of activity; the same remark applies to the gastric follicles, in which the general type of change during secretory activity is very closely allied to those already described for the salivary glands. Langley has found that in the active state the granules decrease in number, the cell becoming clear, and capable of differentiation into a clear outer and a granular inner zone, just as we have seen in the parotid gland; during rest the entire cell becomes granular. The parietal cells during digestion were found to increase in size, but characteristically did not lose their granules. The central cells secrete both the pepsin and rennin ferments, neither of which exist as such in the cells, but as the mother-substances or *zymogens* of the ferments. The formation by the parietal cells of a free acid from the alkaline blood is a special chemical change, the result of selective powers possessed by the cells. In animals, such as the dog, which yield hydrochloric acid, the cells very possibly form it by the interaction of the sodium chloride and the sodium dihydrogen phosphate of the blood; but no satisfactory explanation of how the neutral chlorides are broken up with the formation of hydrochloric acid has yet been given.

Mucin is secreted by mucous glands found in the deep layers of the villous membrane, especially in the region of the fundus; the epithelial cells lining the excretory ducts of the gastric glands also take part in the process. The amount of mucin formed in the stomach of the horse is remarkable; it adheres to the villous coat like unboiled white of egg, and cannot be washed away, even by a powerful jet of water. The amount secreted is unknown, but must be considerable; less is formed during hunger than during activity, and there is less in ruminants than in horses.

Gastric Juice.—It is only lately that a pure sample of gastric juice (but not from the horse) has been available for analysis. Most of the secretions previously examined have been mixtures of saliva, gastric juice, and perhaps other substances. Pavlov devised a method by which the stomach of the dog could be rendered available for physiological inquiry, and a pure secretion was obtained (see Figs. 68 and 69).

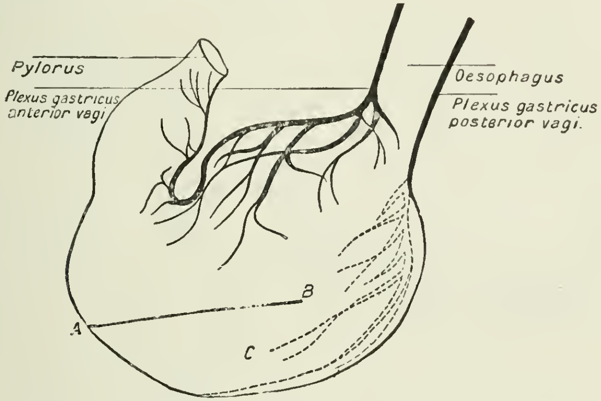

Pylorus
Plexus gastricus anterior vagi
Oesophagus
Plexus gastricus posterior vagi.
B
A
C

FIG. 68.—PAVLOV'S STOMACH POUCH.

A, *B*, Line of incision; *C*, flap for forming the stomach pouch. At the base of the flap the serous and muscular coats are preserved, and only the mucous membrane divided, so that the branches of the vagus going to the pouch are not severed.

Pure gastric juice in the dog is as colourless as water, and possesses a specific gravity of 1·002 to 1·004; it is thin—that is to say, is not mucinous—and of a strongly acid reaction. Chemically it consists of acid and enzymes; it contains 0·4277 per cent. of dried material, of which 0·1325 is ash. The ash contains 24 per cent. potassium, 19 per cent. sodium, and 0·18 per cent. calcium. The acid, which is hydrochloric, amounts to 0·46 to 0·56 per cent., gastric juice being the only secretion in the body containing a free acid. Pavlov states that the total chlorine contents of the secretion are twice the chlorine found in blood, and that he has obtained 5 grammes chlorine from the secretion in $3\frac{1}{4}$ hours—as much as in the entire blood. There are two, perhaps three, enzymes present in the juice—viz., pepsin, rennin, and possibly lipase; the first is unable to act, excepting in an acid medium, and furnishes the only example in the body of this necessary combination of acid and enzyme. Exclusive of the ferments, protein is present. How far the gastric juice of other animals resembles in its composition that of the dog we have no means of knowing, inasmuch as a pure secretion has not been obtained from any other animal; but in all cases an acid and an enzyme are present. The enzyme is invariably pepsin, but the acid is not always hydrochloric. The amount of juice secreted is uncertain; in the dog some 700 c.c. (24½ ounces) have been collected in a few hours, from which we may perhaps imagine that a considerable amount is formed in the stomach of the larger animals.

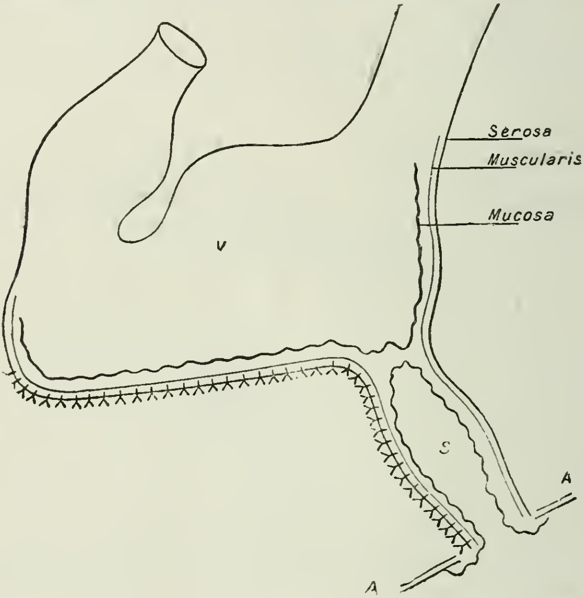


FIG. 69.—PAVLOV'S STOMACH POUCH.

S, The completed pouch; *V*, cavity of the stomach; *A*, *A*, the abdominal wall

Pavlov's experiments on the dog show that the amount of juice secreted is directly proportional to the amount of food eaten; for example, 100 grammes of meat required 26 c.c. of juice, and 400 grammes needed 106 c.c. The same fact was observed on a mixed diet of meat, bread, and milk; if these were increased by half or doubled, the juice was increased in the same ratios.

The gastric juice of the dog withstands putrefaction for a long time; it may be kept for months without undergoing any important change. Not so that of herbivora; the mixed gastric fluids of the horse rapidly putrefy. The antiseptic properties of the dog's juice are attributed to its hydrochloric acid; if this is so, it is additional evidence against the stomach acid of herbivora being hydrochloric. There appears to be no reason why lactic acid should not be formed in herbivora by the marginal cells of the fundus glands, but a source of lactic supply is the carbohydrate of their food.

Pepsin is of a protein nature, though very little is known of it chemically. It exhibits its action best at the temperature of the interior of the body (37° to 40° C.); a low temperature retards its activity, while a high one destroys it. The ordinary commercial product is very impure; it is an extract of the mucous membrane of the stomach to which starch or milk sugar has been added. In physiological work a glycerin extract of the mucous membrane of the stomach suffices; to it is added some dilute HCl. Glycerin has the power of extracting the ferments both from the stomach and from other portions of the digestive tract, such as the pancreas. The pepsin is formed, as we have seen, in the chief cells of the gastric glands as a zymogen or *propepsin*, which becomes pepsin after secretion. The action of pepsin is almost wholly, if not entirely, confined to the protein constituents of food. It converts the insoluble proteins into soluble ones, not by direct transformation, but by several stages. The products intermediate between protein and peptone have received certain names suggestive of differences in their chemical nature, but as to the exact manner and character of these changes a good deal of doubt and of speculation exists.

In the following table the various stages of conversion are indicated in the order in which they are found to occur as determined by slight differences, such as solubility or colour reaction, in the peptonised product, as shown by chemical tests. The table is the one drawn up by Kühne:

1. *The protein as consumed, or native albumin.*
2. *Acid albumin or syntonin.*
3. *Primary proteoses.*
4. *Secondary proteoses.*
5. *Peptones.*

The proteins, having reached the stage of peptones, are now capable of being absorbed. But the conversion from protein to peptone is a most complex one, during which the large protein molecule is converted into simpler products of an infinitely smaller molecular weight, while so great is the complexity that the resulting product, peptone, is in all probability not a single compound, but rather a group of compounds, which resemble each other only in their solubility and their definite reaction to certain chemical tests. There is good reason for thinking that even peptone may not represent the final end-product of the stomach, but that still simpler bodies, to which the name **peptids** has been given, may be formed.

Rennin is the second enzyme found in the gastric juice; it is produced in the chief cells of the gastric glands as a *prorennin*, and is subsequently, on secretion, changed into rennin under the influence of the acid present. This enzyme can be readily obtained from the true stomach of the calf, but not from the pyloric end. Commercially, rennin is used in the manufacture of cheese, a good extract causing very rapid clotting of milk. This process closely resembles the clotting of blood, and, like it, is followed by a contraction of the clot, resulting in a solid substance known as *curds*, and a yellowish fluid, *whey*. The above process further resembles blood-clotting in requiring the presence of a calcium salt. The conversion of the casein of milk into curd is believed to involve two distinct processes: first, the formation of a substance known as *paracasein* by the action of rennin; and, secondly, the action of lime salts on paracasein, by which means the curd is produced. The curdling of milk brought about by the lactic acid organism may be familiarly recognised when milk 'turns sour'; it is not the same as clotting, but represents the precipitation of casein by an acid.

There would appear to be no necessity for animals to possess this ferment after weaning, as milk does not form an article of diet for animals, if we except the chemically altered milk given to the pig. Once the curd is formed, the process of digestion is carried on by pepsin, rennin taking no further part.

Rennin has been described as existing in the pancreas, testis, and in vegetable tissues, but little is definitely known. It is stated that an *antirennin* may be formed in the blood by immunising an animal by injections of rennin, and that the substance produced prevents milk clotting.

Other ferment actions of the gastric juice have been described, such as fat- and starch-splitting. A fat-splitting ferment, allied to pancreatic lipase, may, it is said, be extracted from the gastric mucous membrane of young animals, but of the existence of this ferment there is very little evidence. Protein digestion is the essential duty of the stomach, but in all vegetable feeders maceration of the vegetable fibres is begun also in the stomach as a preliminary measure. A stomach is not essential to life in all animals; in the dog, for example, it may be removed experimentally, for, as we shall see later on, protein digestion is provided for elsewhere. But in the herbivora, especially in ruminants, a stomach is essential. The chief value of the stomach in those animals which can be proved to live without it lies in the preparation of the food for subsequent digestion in the small intestines, for it is quite undoubted that protein previously acted upon by gastric juice is far more thoroughly treated by the pancreatic fluid than protein not so previously acted upon.

Influence of the Nervous System on the Secretion of Gastric Juice.—By means of Pavlov's fistula, it has been proved that the secretion of gastric juice is under the control of the nervous system, the secretory fibres being contained in the vagus. Stimulation of the peripheral end of the divided nerve causes secretion after a slight delay; the cause of the latent period is unknown. No secretion results in consequence of mechanical stimulation of the stomach wall, which is contrary to all previously accepted views. The sight of food, its smell, taste, mastication, and swallowing, are direct excitants of secretion. A secretion so obtained is known as psychical. Pavlov's experiment of 'sham feeding' a dog with a divided œsophagus, the upper end of which was brought outside, has placed this psychical secretion beyond doubt. The animal ate a meal which never entered the stomach, but the effect of which could be ascertained through the fistula. In addition to this reflex secretion, there is another produced by the action of some of the food substances themselves; such substances, known as **secretagogues**, directly stimulate the production of gastric juice, though all foods do not possess this power. Bread, starch, fat, and white of eggs, introduced surreptitiously into a Pavlov's fistula so that the animal does not see them, do not excite secretion; while, on the contrary, meat extract is most effective.

Secretagogues in the products of digestion may also influence the production of gastric juice. This **chemical secretion** is difficult to explain; it occurs after the vagus and all other nervous connections are cut, which suggests that it does not operate through a nervous reflex. It has been shown by Edkins that the injection into the blood of an extract of pyloric mucous membrane, specially prepared, causes a marked secretion of gastric juice. And it is suggested that the chemical secretion above referred to may be produced by the action of the secretagogues upon the pyloric mucous membrane, resulting in the formation of a *gastric secretin*, or *gastrin* (analogous to *pancreatic secretin*, yet to be studied), which, when absorbed into the blood, acts as a chemical excitant, and stimulates the production of gastric juice. The secretins belong to the class of bodies now referred to as *hormones*.

Pavlov believed that the quantity and quality of the gastric juice will be found to depend on the character of the food, so that while in some cases an average production is obtained, in others a stronger or weaker fluid is poured out, depending upon the work to be done, the regulation of which is probably a specific action on the part of the food itself.

Each article of diet in a meal of meat, bread, and milk, taken separately, produces not only a definite rate of secretion of gastric juice, but also an alteration in the quality of the ferment suited to the work it has to perform. Thus flesh or bread causes a maximum secretion during the first hour of digestion; milk during the second or third hour. The greatest digestive powers of the gastric juice are found to occur with a meat diet, while the weakest proteolytic action occurs with milk.

If an animal fed for weeks on a bread-and-milk diet be suddenly placed on meat, the power of dealing with protein is at first weak; the juice is in sympathy with a starchy rather than with a protein diet. If another change be made when the meat diet is being satisfactorily dealt with, and the animal put back on bread and milk, the whole process has to be reversed, and the glands this time brought into accord with a starchy rather than with a protein diet.

It is true this observation has been made on the pancreatic juice, but doubtless what is true for it is true for other digestive secretions. Further, we have overwhelming proof in everyday management of horses that sudden changes in diet are productive of disease. Whether the above facts regarding digestive juices and changes in diet are explained by what we know of the function of chemical excitants—'*hormones*'—remains to be proved.

Such is the modern account of stomach digestion. We appear to have approached appreciably nearer to a better understanding of the circumstances attending digestive troubles in the horse, and, as we shall have to point out again in dealing with pancreatic secretion, Pavlov's work explains why a sudden change of a long-continued diet is bad, and is, as we know, followed in horses by disastrous consequences.

Starch Conversion.—There are other changes occurring in the stomach independently of peptonisation or of gastric juice. If a horse be fed on oats and the stomach fluid examined, it will be found to contain an abundance of sugar. The sugar, we suggest, is produced from an enzyme in the starch of the grain, and is not, according to our observations, caused by the action of saliva. Abundant saliva exists in the stomach, but it will be remembered that in the horse we have never succeeded in getting it to give any evidence of starch conversion. The question, therefore, is, What is the cause of this formation of sugar? Pitchford's observations prove that in some horses it may be due to the saliva, but in those whose secretion is non-amylolytic a ferment in the grain explains the observed facts, and a starch converting enzyme has been shown to exist in cereals. The whole of the starch is not converted in the stomach, for distinct evidence of unaltered starch can be obtained in the first portion of the small intestines. Further, some of the starch is no doubt converted into lactic acid, and the presence of this acid in the proportion of 2 per cent. does not in any way inhibit the amylolytic action. If oats provide their own starch-converting enzyme, we have here the strongest argument against giving boiled food for horses—a practice we believe to be deleterious, or even dangerous.

Fats are not acted upon in the stomach, though the envelope surrounding the fat globule is digested, and the fat set free.

Cellulose fermentation is considered by Tappeiner to occur in the left sac of the stomach, and when marsh-gas has been found in this organ, it is the result of cellulose decomposition. Brown* has shown that the destruction of the cell wall of oats and barley occurs in the stomach, where the wall is dissolved by a cyto-hydrolytic ferment *pre-existent in the grain*; the changes occur with extraordinary rapidity in the stomach of the horse. The researches of this observer on a cellulose-dissolving ferment are of the greatest interest to the veterinary physiologist, and of considerable practical importance.

Periods of Stomach Digestion in the Horse.—Stomach digestion in the horse has been divided by Ellenberger and Hofmeister into certain periods corresponding to definite chemical changes in the food. For example, it is said that during the two first periods, which between them last two and three hours, starch conversion, lactic acid fermentation, and protein conversion to a limited extent take place. In the third period mixed digestion of starch and protein occurs, while in the fourth and last period only protein digestion takes place. The third and fourth periods may together last four hours and upwards. We must be careful to avoid regarding the account of these periods as based on some rigid law; they are very variable in duration, owing to causes we have previously considered, and run imperceptibly into each other. With this caution we give the following periods at which gastric digestion is said by Ellenberger and Hofmeister to be at its maximum in the horse:

After a moderate feed digestion is at its height in 3 or 4 hours.
,, full ,, ,, ,, ,, 6 to 8 ,,
,, an immoderate ,, delayed still longer.

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* 'On the Search for a Cellulose-dissolving Enzyme,' H. T. Brown, F.R.S., *Journal of the Chemical Society*, 1892, p. 352.

Stomach Digestion in Ruminants.

The stomachs of ruminants are divided into three compartments and one true stomach. The compartments are the rumen, reticulum, and omasum. The true stomach is the abomasum (see Fig. 70).

The **Rumen** is divided into four sacs by the constrictions produced in its wall by large muscular bands, which on the interior of the organ are of immense thickness, and well deserve the name of pillars. The interior of the organ is lined with a well-developed mucous membrane, covered with pointed papillæ, 3 to 9 mm. in length, excepting where the muscular pillars are most prominent. A few small glands are described as existing in this mucous membrane, but they form no digestive secretion. The rumen communicates freely with the reticulum; by means of the œsophageal groove it is connected with the omasum, and it naturally connects with the œsophagus. Material in the rumen can do one of three things—pass into the reticulum, into the omasum, or into the œsophagus. The way to the omasum and œsophagus is via the œsophageal groove.

The **Œsophageal Groove** (see Fig. 71) is a canal which runs from the termination of the œsophagus on the inner wall of the reticulum to the omasum. Guarding it on the aspect presented towards the rumen are two fleshy lips, thick and overlapping below, thin above. These lips approximate so closely that the groove can only be discovered by separating them. The object of the lips is to open and permit the passage of material direct from the œsophagus to the rumen or reticulum, or from these to the œsophagus or omasum. Further details are given on p. 210.

The capacity of the rumen is enormous: 100 litres (22 gallons) can be stored in it in the ox; 4 to 6 litres (8¾ gallons) in the sheep. Its muscular bands are arranged in two diameter-like girdles, and their function is very obviously to contract on the contents. All solid food, on being received from the mouth, enters the rumen; all fluid substances may enter any or all of the compartments, or they may proceed to the abomasum via the omasum, as is the case in the calf, or they may go to the rumen or reticulum, as most fluids—viz., saliva and the water consumed—do in the adult. Colin, having placed his hand in the stomach, assured himself, through a window in the abdominal wall, that during the first mastication very little passes to the omasum and abomasum, and that fluid only. Without fluid the rumen can do no work; cut off the supply, and rumination ceases. This explains the necessity for the enormous salivary secretion in these animals. The rule appears to be that the greater part of the fluid arriving in the stomach is divided between the first and second compartments, the overflow from these passing in to the omasum and abomasum.

As food arrives in the rumen it passes into what Colin has described as the lower storey, a part which never empties itself. It consists of the usual coarse ingesta and fluid. As the stomach fills, the mass extends into the upper storey, the stomach dilating, and finally the reservoir becomes full to the roof, though not tightly packed. The last arrival in the rumen is naturally received in the anterior extremity of the left sac, and from here it passes through all hemispheres of the rumen. Material from the posterior part of the rumen makes its way forwards towards the œsophageal opening for remastication, and there can be no doubt that the mass in these sacs is actually revolved, for material capable of identification, if introduced into the stomach through a wound in the abdominal wall, gradually disappears, and returns to the same place in from twelve to twenty-four hours.

Colin, through the window in the abdominal wall, was able, by illumination, to inspect the interior of the rumen during digestion, and while food was still arriving in the compartment. He observed that the level of the mass varied from moment to moment, rising and falling alternately; he could even see a portion rise up out of the mass, detach itself, and pass backwards. At other times the detached portion moved forwards; in either case it disappeared into the body of the organ, and was churned up again later on. During rumination or when fluids are swallowed this oscillation of the mass is most energetic, and, as Colin expresses it, the flow and return flow are most interesting to witness. They induce the most complete mixing of the contents, that which was at the top passing to the bottom, while the material at the bottom passes to the top. Evidence of the completeness of the churning movements of the rumen is afforded by the perfectly spherical ‘hair balls’ which are sometimes found there. Stimulation of the mucous membrane of the rumen provokes contraction of the walls, especially of the muscular pillars.

The contents of the rumen are alkaline generally, more markedly so in the lower than in the upper parts, where, in fact, a slightly acid reaction may be obtained from food fermentation. Very frequently the nature of the reaction is doubtful. The alkaline reaction is due to the saliva, for there is no secretion from the wall of the rumen.

The **Function of the Rumen** is to retain the food for remastication, to macerate all fibrous substances and render them fit for cellulose digestion, and to act to a limited degree on carbohydrate and nitrogenous matters. Cellulose is by far the most important food substance dealt with; no cellulose ferment is at present known, but there are ferments probably contained in the food which, together with decomposition, under the influence of heat, moisture, and bacteria, act energetically on cellulose. In consequence of its digestion gases are formed—carbonic acid, sulphuretted hydrogen, hydrogen, nitrogen, and marsh-gas in quantities. In excess it is these gases which produce the pathological condition known as tympanites. The carbohydrates are attacked by organisms which convert appreciable quantities of starch and cane sugar into glucose, while, under the influence of microbes of putrefaction, fermentation is produced in the nitrogenous substances of the food, slowly converting them into peptone. The acid found in the lower sac results from lactic acid fermentation, while acetic, butyric, and other acids are present. The acids are always limited in amount, excepting under digestive derangement, when they become excessive and are associated with tympanites.

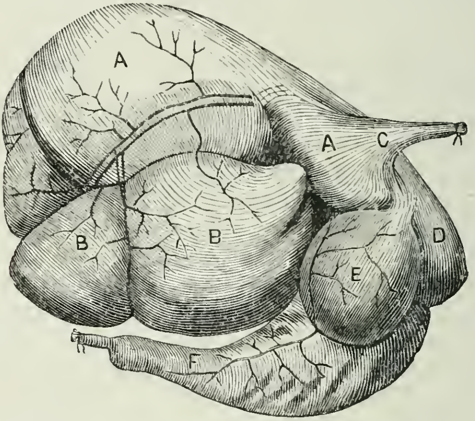

Fig. 70.—The Gastric Compartments and True Stomach of Ruminants (Colin).

C, The œsophagus; A, A, left hemisphere, B, B, right hemisphere of the rumen; D, the reticulum; E, the omasum; F, the abomasum.

The rumen never empties itself; even after prolonged starvation it contains food. In young ruminants digestion occurs principally in the abomasum, the other compartments being rudimentary; when the young animal is placed on solid food, it is remarkable how soon the rumen, reticulum, and omasum are developed, and the process of remastication established.

The **Reticulum,** or second gastric reservoir, is a small one placed anteriorly and inferiorly resting, in fact, on the sternum (see Fig. 72). Its capacity in the ox is 2 litres ($3\frac{1}{2}$ pints), and in the sheep 0·2 litre (0·35 pint). It communicates with the rumen by a large opening formed by a constriction of its walls; the bulk of the organ lies below this opening. Over the lip which separates the two chambers fluids and solids may pass in either direction. The reticulum communicates with the œsophagus viâ the œsophageal groove, under the opening of which it is placed like a sac, while by means of the same groove it communicates with the omasum. The muscular coat of the reticulum is largely striated, being a continuation of the œsophagus, and, in consequence, the movements of the compartment are not only powerful, but energetic. The mucous membrane on its interior, being arranged in polyhedral cells 10 to 15 mm. in depth, closely resembles a honeycomb. In these cells stones, gravel, and foreign bodies may frequently be found, the latter in many instances penetrating the heart.

The contents of this compartment are fluid and alkaline, the fluid being derived from that swallowed, and from the rumen; the alkaline reaction is due to the saliva, for, so far as we know, the mucous membrane possesses no secretory activity. The fluid in the reticulum is of use in rumination, and is forced into the œsophagus by a contraction of the walls of the viscus; it may also be forced into the rumen. Colin, with his hand in this sac—the presence of which produced energetic contractions—found the fluid poured over his hand, flooding the contents of the rumen. In order that fluid may be retained in this bag, the openings out of it are situated considerably above the base of the organ; and, further, the reticulum is so situated relatively to the rumen that it receives the overflow of fluid from that compartment when the latter contracts.

Ellenberger is of opinion that the reticulum regulates the passage of food from the first to the third compartment, and from the rumen to the œsophagus. In transferring the contents of the rumen to the omasum, the reticulum contracts and forces the material into the œsophageal groove. Flourens showed that the reticulum was not essential to rumination, for he excised it in a sheep, and rumination was not interfered with.

The **Omasum**, or third compartment, is quite different from those hitherto examined. Placed between the reticulum and abomasum, the viscus does its work with its contents inverted. The openings into and out of a stomach or diverticulum are generally above the portion holding the contents, but in the omasum the contents are above the openings which lead into and out of it. The omasum defies the laws of gravity.

This third compartment communicates anteriorly with the second and posteriorly with the fourth, by means of a canal three or four inches long, which runs obliquely backwards, downwards, and to the right. It is over this canal that the structure of the omasum is placed. The interior arrangement of the organ is most singular, being composed of several large leaves running the length of the organ; between these are smaller leaves, and between these a third and then a fourth series. Altogether about one hundred laminæ of variable size are found in the compartment. The leaves are papillated, the papillæ at the reticulum end being large, horny, and pointed; towards the omasum end they lose the pointed character and become warty. Ellenberger, who has specially worked out the physiology of this organ, and whose description we intend to follow, describes the anterior papillæ as resembling the teeth of a harrow, the posterior papillæ those of a file. In all cases the papillæ are arranged with their free ends pointing towards the abomasum, the object of this being to direct the food towards the abomasum, and prevent its reflux towards the reticulum when the walls of the organ contract.

The food may find its way into the omasum, either directly from the œsophagus after remastication, or from the first or second compartments. It is probable that its chief source of supply is directly from the œsophagus, the omasum being drawn forwards towards it by a contraction of the pillars of the œsophageal groove, by which means communication with the rumen and reticulum is cut off. Normally the reaction of the contents of the omasum is neutral; if found acid, this is due to regurgitation from the true stomach.

We have the authority of Ellenberger for saying that the organ secretes no digestive fluid, nor does it absorb. It is peculiar in possessing a separate source of nerve-supply, stimulation of the pneumogastric producing contraction of all the compartments but this. Further evidence of an independent nerve-supply is furnished by the fact that after death the walls of the other stomachs relax, but that of the omasum remains contracted.

When the food arrives at the omasum the opening leading to the abomasum is closed, and by means of the horny papillæ at the reticulum end of the organ the material is divided and directed towards the leaves, the œsophageal groove at the same time closing in order to prevent a reflux. The presence of the food then causes a reflex contraction of the leaves, by which they are rendered rigid and tense, and advance to meet the mass. The leaves having been drawn forward, the fibres now relax, by which movement the food is carried back with them. The direction of the papillæ on the leaves prevents the material from falling out of the chambers formed between the leaves, while the curve of the organ enables the leaves to give each other mutual support, like the bricks in an arch, so that no muscular effort is required to maintain the food in position. The walls of the omasum are strong, the circular fibres being three or four times as thick and powerful as those longitudinally placed; contraction of the walls is almost constantly occurring. In this way the contents of the omasum are moved towards the fourth stomach, the position and direction of the papillæ preventing them from travelling in the other direction. Each contraction drives the ingesta not only towards the omasum, but more completely between the laminæ of the deeper system. These leaves take no part in emptying the omasum; their function is to advance and meet the incoming matter, then to raise it to the system of channels formed by the series, and finally, by means of their papillæ, to further grind down and reduce insufficiently remasticated food. This grinding or rasping down is effected by the leaves becoming shorter, thicker, and stiffer; the papillæ on them are drawn through the mass like the teeth of a harrow. The movements of the leaves are not simultaneous, but successive; while one is passing in one direction, its fellow is travelling in the opposite direction, so that rasping of the food is continually going on, and this is evident from the fact that the contents are much finer at the abomasum end than at the reticulum end of the organ. Ellenberger, therefore, speaks of the third compartment as a triturating apparatus, a masticatory stomach, the contents of which are dry because the fluid part is being constantly strained off.

With illness rumination ceases, and the chief supply of fluid to the omasum is then cut off—viz., the saliva, which is re-swallowed during rumination. As no fresh ingesta and very little fluid is entering the omasum, the contents rapidly become dry and caked.

The **Abomasum,** or true digestive stomach, is the only compartment secreting gastric juice. In the abomasum proteins are converted into peptones, the region of the cardia being in this respect more active than that of the pylorus. Ellenberger states that starch is also digested, and that this precedes protein digestion. In the fourth stomach of the calf a milk-curdling ferment (rennin) exists, which has already been dealt with.

Stomach Digestion in the Pig.

The stomach of the pig is peculiar; it is a type between the carnivorous and ruminant, and is divided by Ellenberger and Hofmeister into five distinct regions, which do not all possess the same digestive activity.

The gastric juice of the pig contains for the first hour or two of digestion lactic, and afterwards hydrochloric, acid; pepsin is present, and, it is said, a ferment which converts starch into sugar. In the pig, according to the above observers, the process of digestion is not the same in all regions of the viscus; one may contain hydrochloric acid, another lactic; one may be abundant in sugar, while this may be absent elsewhere. The first stage of digestion is starch conversion; the second is the same, only more advanced; the third stage is starch and protein conversion, both processes occurring at the cardia, but only protein conversion taking place at the fundus; lactic acid is present in the cardia, and both lactic and hydrochloric acid in the fundus. In the fourth stage starch conversion is nearly complete, while hydrochloric acid predominates in all the regions, and protein conversion is general.

Stomach Digestion in the Dog.

Very complete knowledge of the physiology of the dog's stomach exists, for nearly all the work undertaken to elucidate the physiology of the human stomach has been effected on the dog. We have summarised some of this knowledge in the previous pages in treating of gastric juice.

In the stomach of the dog and cat digestion occurs mainly in the pyloric dilatation or antrum, which is from time to time cut off from the rest of the stomach by the pyloric ring or transverse band (not to be confused with the pyloric sphincter), so that the general body of the stomach acts mainly as a receptacle, passes, from time to time, material into the antrum for chyme conversion, and then ejects it into the intestines. The length of time material lies in the stomach depends upon its nature and consistence; both carbohydrates and fats escape into the intestines more readily than proteins. The time appears to depend also upon the strength of acid present. A weaker acid sufficing for non-protein food is more rapidly neutralised in the small intestines, and the opening of the pylorus appears to depend upon impulses passing from the duodenum as soon as the last received acid supply has been neutralised in that bowel.

A flesh diet requires very little saliva and practically no mastication, but its digestion is slow, in spite of the fact that it is taken in a form closely allied to that in which it is assimilated. Colin states that it takes a dog twelve hours to digest an amount of meat which it could eat at one meal. The substances most difficult of digestion are tendons and ligaments, but of these digestion is facilitated by boiling; liver and flesh are best given raw, as cooking interferes with their digestibility. The gastric juice of the dog is fully described at p. 193.

Absorption from the Stomach.—The needful changes occurring in the stomach having been considered—we now refer principally to the stomach of the horse—the next step is to inquire into the proportion of food so altered as to be rendered fit for absorption.

Experiment shows that in the stomach 40 to 50 per cent. of the carbohydrates has been converted into sugar, whilst 40 to 70 per cent. of the proteins has been converted into peptones. When food has been long in the stomach, not more than 10 per cent. of the proteins escape being peptonised. In ruminants probably the greater part of the digestion of the food substance is carried out in the gastric compartments and stomach, leaving comparatively little for the intestines to perform.

In spite of the changes which occur in the stomach, it has been proved by the experiments of Colin that *no absorption occurs from this organ in the horse*. It would be useless to recapitulate all his experiments; strychnine was generally employed, and he found that, so long as the pylorus was securely tied, no symptoms of poisoning occurred when the alkaloid was introduced into the stomach, no matter how long it was left there, but that when the ligature was untied, and the contents of the stomach passed into the intestines, poisoning rapidly followed. These remarkable results were obtained by him so often, and under such varying conditions, as to leave no doubt as to the accuracy of the observations. Strychnine experiments are not altogether free from objection, but in view of these results we can only surmise that no absorption of sugar or peptones occurs in the stomach. On the other hand, what becomes of the peptones is certainly very mysterious; the writer has never found any in the stomach contents, no matter at what period of digestion the examination was made, and if they are not absorbed in the stomach they must pass very rapidly into the intestines and enter the vessels at once, as no peptone can be found in the small intestines. Colin attributes the absence of absorption from the stomach in the horse to the small area of the mucous membrane, which, he says, cannot be secreting gastric juice and absorbing at the same time. He attributes the non-absorption of poisons in the empty stomach to the thick layer of tenacious mucus which, as we have previously mentioned, covers the villous stomach of the horse. Colin's experiments also show that there is little or no absorption from the abomasum of ruminants. On the other hand, there is absorption from the stomachs of the dog and pig. Recent experiments on the dog show that absorption does not take place readily from the stomach. Water taken alone is, practically speaking, not absorbed at all; sugars and peptones are absorbed only when in sufficient concentration, while fats are not absorbed.

Self-Digestion of the Stomach.—A question which for a long time gave rise to energetic discussion was the reason why the stomach during life does not digest itself, seeing that the action of its secretion is so potent that portions of living material, legs of frogs, ears of rabbits, etc., if introduced into it, are readily digested, and that post-mortem digestion of the stomach in some animals is far from rare. The walls of the stomach are not singular in possessing a specific resistance to a digestive fluid. The small intestine is immune to trypsin, which, if injected under the skin, digests the tissues and produces ulceration. Fæces and urine are very irritating, unless, so to speak, in their own home. The bladder never shows any sign of irritation from the presence of urine, but if it be paralysed, and the urine, in dribbling away, falls on the skin, the part in time ulcerates, and very early becomes excoriated. Even tears running over the face, in cases of obstruction of the duct, cause the skin to ulcerate. In spite of the action of gastric juice, ' bots ' live in the stomach for months, and, unfortunately, are never digested. Parasites of the digestive tract enjoy the same immunity from digestion that the membrane of the canal possesses.

It is now generally believed that the immunity enjoyed by the tissues in contact with active or irritating secretions is due to the local formation of an antibody. That in the stomach has been named *antipepsin*, and its function is to neutralise the digestive action of the gastric juice on the living wall.

We have never yet met with post-mortem digestion of the stomach in the horse; whether this be due to the horse's acid being mainly or wholly lactic cannot be definitely stated.

The Gases of the Stomach.—The nature of these largely depends upon the food—for example, green food is most productive of gas, owing to the active fermentation it undergoes. Traces of oxygen, a quantity of carbonic acid, and variable amounts of marsh-gas, sulphuretted hydrogen, hydrogen, and nitrogen, are found. The oxygen and nitrogen are derived from the swallowed air, the carbonic acid is derived from the fermentation of the food and the action of acids on the saliva, while the marsh-gas is obtained by the decomposition of cellulose.

The gases from the intestines of the horse and rumen of the ox are very commonly inflammable, and burn with a pale blue flame. This is due to marsh-gas, which may be readily ignited when mixed with a due proportion of oxygen.

Vomiting and Rumination.

Vomiting amongst solipeds and ruminants is rare, but the act is common in the dog and pig.

The explanations given as to why the horse does not *ordinarily* vomit are various: (1) The thickened and contracted cardiac extremity of the œsophagus; (2) the oblique manner in which the latter enters the gastric walls; (3) the dilated pylorus lying close to the contracted cardia, so that compression of the stomach contents forces them into the duodenum; (4) the cuticular coat thrown into folds over the opening of the cardia; (5) muscular loops encircling the cardia, the contraction of which keeps the opening tightly closed; (6) the stomach not being in contact with the abdominal wall. All these and other reasons have been assigned as the cause of non-vomiting in the horse. Yet on turning to ruminants, which also normally do not vomit, we find the stomach, gastric compartments, and œsophagus freely communicating, the largest reservoir lying in contact with the abdominal wall, the cardia freely open, the œsophagus of great size, and, still stranger, the animal possessing the ability, under the control of the will, to bring up food from the stomach as a normal condition, and yet unable to vomit. It is evident, therefore, that all these theories, taken together, are not sufficient satisfactorily to account for the absence of vomiting, and we are bound to suppose that the vomiting centres in the medulla of both horse and ox are either only rudimentary or very insensitive to ordinary impressions.

Vomiting in the horse is no doubt seriously interfered with by the thickened œsophagus, contracted cardia, and the arrangement of the muscular fibres. The folds of mucous membrane filling up the orifice could offer no serious obstruction to a distended stomach, for it is known that even when this membrane is dissected away post mortem, a stomach will burst rather than allow fluid or air pumped in at the pylorus to escape at the cardia, unless the muscular fibres surrounding it be partly divided. Vomiting in the horse is generally indicative of ruptured stomach, and much has been written as to whether it occurs before or after rupture. From no inconsiderable experience of these cases, the writer has arrived at the conclusion that it may occur at either time, and that a horse may vomit though a rent 7 or 8 inches long exists in the stomach wall.

Dilatation of the cardia and œsophagus is essential to the act of vomiting in the horse, and in all cases where vomiting occurs during life the cardia is so dilated that two or three fingers may readily be introduced into it. It is perfectly possible for a horse to vomit and recover (showing that it had not a ruptured stomach), and it is not unusual to have attempted or even actual vomition when the small or large intestines are twisted. Vomiting in the horse is not as a rule attended by any distressing symptoms; the ingesta dribble away from one or both nostrils; occasionally an effort is made on the part of the patient, the head being depressed to facilitate expulsion, but more than this is very rarely seen.*

It is important to notice in connection with the subject of vomiting that agents such as tartar emetic, ipecacuanha, and apomorphia, which excite vomiting by their action on the cerebral centre, have no effect on the horse or on ruminants, nor does the horse vomit as the result of sea-sickness, though he suffers extremely from it. Why vomition should be more frequent in horses with a ruptured stomach than when the organ is whole is a fact we cannot explain.

In those animals where vomiting is a natural process, the three important factors are—The dilatation of the cardia by active contraction of the longitudinal fibres of the œsophagus, pressure on the walls of the stomach by a contraction of the diaphragm and abdominal muscles, and closure of the pylorus. But there is some evidence to show that the stomach itself is not passive; it is true Majendie produced vomiting after he had replaced the stomach by a bladder, but under normal conditions there appears no reason why the stomach wall should remain quiescent, and in the cat it has been observed that during vomiting a strong contraction of the pyloric end of the stomach occurred, shutting it off from the cardiac portion. We may here have one explanation of ruptured stomach in the horse, which is supported by the view put forward on p. 181 of the influence of the duodenal trap.

The œsophagus in ruminants has its inner layer of fibres spirally arranged in double obliquity; the tube is wider at its termination than in the anterior part. On entering the gastric reservoirs, it forms a groove, previously described (see description, Fig. 71), which brings it into connection with all the compartments. In this way material coming down the œsophagus may enter any of the reservoirs, the choice being determined by the condition in which it is swallowed.

The lips or pillars of the œsophageal groove are composed of involuntary muscular fibres, arranged longitudinally and transversely by means of which arrangement the groove can be shortened and constricted. By a contraction of the pillars, the omasum may be drawn forward and brought nearly into apposition with the œsophagus. By relaxation of the pillars the œsophagus is made to communicate with either the first or second reservoir. Fig. 72 shows the rumen and reticulum in position.

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* The only case of vomiting the writer has seen in the horse which resembled that presented by the human subject was in a case of volvulus of the small bowels. The horse was lying on his chest with the muzzle tended, the ingesta gushed in a stream from both nostrils, and a sound accompanied the effort.

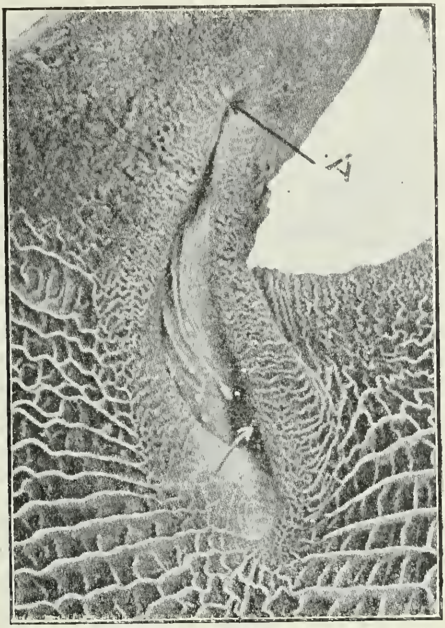

FIG. 71.—THE ŒSOPHAGEAL GROOVE FROM THE RETICULUM. THE GROOVE IS SHOWN WITH ITS LIPS SEPARATED. FROM A PHOTOGRAPH. (SISSON.)

A, opening of œsophagus. The arrow below points to the reticulo-omasal orifice. The groove is about 7 inches long, and though vertically placed in the reticulum, there is a slight spiral twist in the canal. The groove is lined by mucous membrane similar to that of the œsophagus, and on this membrane at the lower part there are some horny papillæ.

The reticulo-omasal opening is about $1\frac{1}{4}$ inches in diameter. The groove continues from here and passes along the floor of the omasum to the abomasum. The length of this channel, which gradually increases in width, is about $3\frac{1}{2}$ inches, and it opens into the abomasum by an orifice 4 inches in diameter. As the abomasum lies on the floor of the abdomen its course is backwards, downwards, and to the right.

The groove from the cardia to the abomasum may be regarded as a portion of modified œsophagus, provided with a slit in its side capable of opening and closing, and its further portion as an open channel or gutter on the floor of the omasum.

The œsophageal groove is represented as open, though normally its lips cover it so perfectly that it requires looking for. The close proximity of the reticulum to the heart will be observed, and in this connection see the remarks on p. 203. At one time it was considered that the œsophageal groove took an important share in rumination, but the question was decided by Colin in his usual thorough manner. He stitched the pillars together, and found this did not interfere with the process. Prior to this experiment it was believed that the lips formed the bolus, and then passed it into the œsophagus. Colin, with his hand in the stomach, introduced ingesta into the canal, but could not succeed in getting the lips to grasp and carry it into the œsophagus. Additional proof of this point is furnished by the llama, which ruminates and has but one pillar to the groove.

After the food has remained sufficiently long in the rumen, exposed to a slow churning movement and to the action of the various bacteria, which cause softening and ultimately digestion of the cellulose, it is returned as a bulky mass to the mouth for remastication. That which is ready is slowly pressed forward towards the œsophagus, the diaphragm by contracting forms a partial vacuum in the chest, and material is drawn into the œsophagus under the influence of this vacuum, assisted, perhaps, by a contraction of the abdominal walls, but not by the walls of the rumen, as supposed by Colin. Chauveau was responsible for this theory, and Toussaint placed it to the test of experimental inquiry by means of various air-chambers introduced into the œsophagus and respiratory passage, which recorded their movements on a revolving drum.* In this way it was found that immediately preceding a regurgitation the glottis closed, the diaphragm contracted, and a partial vacuum was formed in the chest. According to these observers, the contraction of the abdominal muscles is purely passive, and depends upon the displacements caused by the oscillation of the diaphragm. It is certainly a fact that the sudden contraction of the abdominal wall is scarcely seen in the ox, though it is somewhat clearer in the sheep, and very evident in deer, so that, as opposed to the original view of Colin, and what the observer can see for himself, the contraction of the abdominal muscles would appear to take no active share in the phenomenon.

If a tracheotomy be performed, rumination is not prevented, though the glottis can no longer close; the thoracic walls, which are ordinarily passive during the phenomena, now take on a vigorous inspiratory activity, and so assist the diaphragm. If the phrenics be divided the diaphragm is paralysed, but rumination is not abolished; other inspiratory muscles intervene, and the process is carried out, though with difficulty. If the distal end of the divided phrenic be stimulated, the diaphragm contracts and regurgitation takes place, while if at the moment of stimulation the nostrils and mouth be momentarily closed, there is a violent expulsion of ingesta to the distance of several feet.* The modern theory of rumination, then, is that it is produced by aspiration within the thorax causing a negative pressure in the œsophagus, and thus 'drawing out' the ingesta from the rumen, the walls of that organ taking no share. In fact, during the act of regurgitation, they are quiescent.

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* 'Éléments de Physiologie,' F. Laulanié, 1905.

In this way the semi-solid ingesta from the rumen, together with fluid from the reticulum, is sucked into the œsophagus; here the bolus is cut off by the cardiac end of the tube, and by reversed peristaltic action the bolus is conveyed to the mouth, the soft palate being raised, thus cutting off the posterior nares. In passing under the velum the liquid portion is squeezed out, and is at once reswallowed, passing to the third compartment, while the solid material is ground. If the left abdominal wall be auscultated during rumination, certain sounds may be heard. One of these Colin describes as resembling a crepitant lung râle, and is due to the disengagement of gas in the rumen; another is a friction sound resembling that heard in pleurisy, due to the gliding motion of the gastric reservoirs against the abdominal wall and diaphragm; and a third sound is heard at the moment the fluid returns from the mouth. Gurgling sounds may also be heard over the œsophagus in the neck at the moment of swallowing.

The bolus in the mouth may weigh from 100 to 120 grammes (3 to 4 ounces), and it is projected into this cavity with such force that if the mouth is open it may drop out. Its remastication occupies about fifty seconds; it is then reswallowed, and passes to the third compartment, or, if not sufficiently comminuted, it returns to the rumen, and is once more remasticated.

The ascent and descent of the bolus in the neck may be readily seen, and Colin has estimated that each of these requires 1·5 seconds, while an equal period is required for the formation of a fresh bolus. On this data, from the time the bolus is prepared until its return must occupy 54·5 seconds. One minute may be taken as sufficiently near. Rumination is, therefore, a slow process, and occupies at least seven hours out of the twenty-four. The length of time an animal will continue when ruminating to use the jaws in one direction is remarkable; from the effort involved frequent changes of direction might have appeared to be necessary, but such is not the case. One-quarter to half an hour's mastication on one side may be performed.

The animal prefers a recumbent position for the process, but draught oxen may be seen ruminating in the yoke, and camels while carrying their burdens.

The share taken by the reticulum in rumination is mainly the supplying of fluid to the mass, but rumination can occur even after the removal of the reticulum. Unlike the rumen, it is capable of sudden contractions. A certain distension of the rumen is absolutely necessary; though this organ never empties itself, it must contain a fair amount of food before rumination begins; further, it must contain a considerable quantity of fluid. If the salivary flow which so largely contributes to this fluid be diverted, remastication becomes difficult, though for a day or two rumination may be carried on; later it begins to fail, and it is only by a great effort that food can be passed into the œsophagus. Colin's experiment in this direction showed that by the thirteenth day

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* Laulanié, *op. cit.*

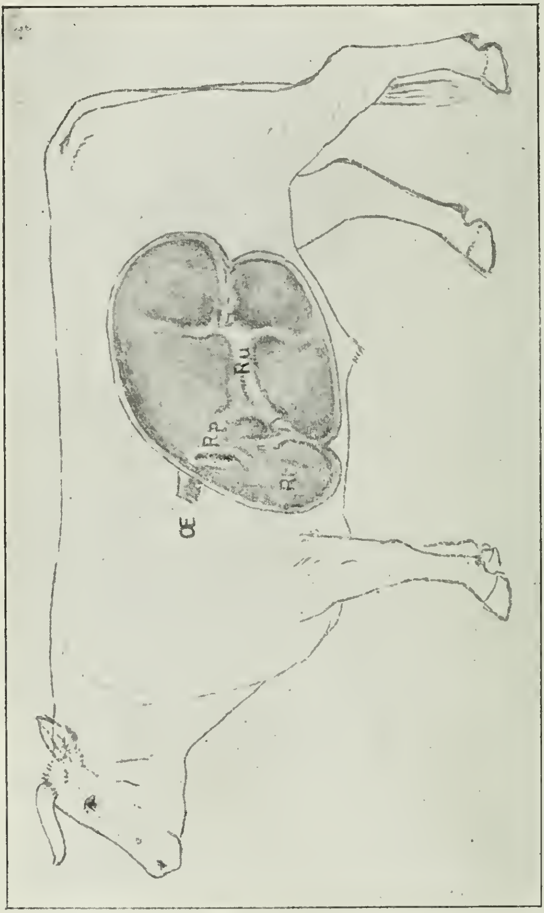

Fig. 72.—The Position of the Œsophageal Groove in the Living Animal.

Ru, Rumen: the lettering is placed on the muscular pillars; Rt, reticulum; Œ, œsophagus; Rp, right pillar of œsophageal groove: both pillars are represented as if held apart in order to show the canal.

rumination was no longer possible. It has been shown that the parotids of the ruminant are always in a state of activity, and the object of this continuous secretion is to insure the function of rumination being duly carried out.

An animal alarmed or disturbed at once ceases to ruminate, and one of the first signs of ill-health is that the function is suspended.

Rumination is a reflex nervous act, the centre for which probably lies in the medulla. If, as we have seen, the phrenics be divided, rumination is carried out with great difficulty, and only by an extra effort of the inspiratory muscles; if the vagi be divided, or the spinal cord in the mid-dorsal region, rumination is no longer possible.

Movements of Food in the Stomach.

A good deal of exact information as to the manner in which the stomach behaves in dealing with its contents has been obtained by means of direct experimental inquiry. Colin, in the case of the ruminant, introduced his arm into the organ through an external opening. In the horse, carefully conducted feeding experiments have helped to show what occurs from hour to hour, but it was not until the X rays were employed that the process could be seen occurring in the intact living animal.

If a cat be fed on a diet liberally mixed with bismuth, the process of digestion can be watched by X rays, owing to bismuth being opaque to these rays. Within a few minutes of the entry of food into the stomach, contractions, which begin at the middle of the organ and end of the pylorus, are started. As digestion advances the contractions become stronger and regular, occurring at intervals of about ten seconds, and travelling to the pylorus, which is reached in twenty seconds. Periodically the pylorus is relaxed, and chyme forcibly propelled into the duodenum; after each discharge it closes, and in course of time the process is repeated. All idea of a churning motion occurring in simple stomachs has now been abandoned; it was difficult to disprove, except in the case of the horse, until X rays were employed. In the horse the arrangement of the food in the stomach in strata as received never left any doubt that churning took no part in the process of stomach digestion in this animal. It will be observed that the cardiac end of the stomach of the cat takes apparently no share in the movement, and it is probable that in most animals this end plays but a passive part. In the horse, in fact, it may almost be regarded as an œsophageal dilatation

If the abdominal cavity in a recently destroyed horse be rapidly opened, it may be possible to see the stomach at work. Its peristalsis is slow, rather more deliberate and less energetic than intestinal peristalsis, and not infrequently hour-glass constrictions may appear, though not to a marked degree. Many observations may be made before gastric peristalsis is seen; unlike intestinal peristalsis, it is not always present after death.

The mechanism controlling the opening and closing of the pylorus is by no means clear; solid bodies are denied a passage for some time, and even for chyme the pylorus does not open with every contraction wave which passes over the stomach. A bullet administered as a bolus was found in the stomach thirty-six hours later, though the animal had in the meantime been fed, from which it seems certain that the pylorus is capable of deciding what should and what should not pass. Yet in the case of the horse some modification in this statement must be made, for, as has been shown, owing to the small size of the stomach and the bulky nature of the food in an organ already filled, an amount passes out at one end equal to that being taken in at the other, and where this mechanism fails disease at once arises.

Liquids rapidly pass out of the stomach of the horse; the large quantities of fluid required by this animal could not be contained in the stomach. In fact, if auscultation be practised while an animal is drinking, water may be heard passing along the duodenum below the right kidney.

Little of what has just been said applies to ruminants. The movements of the stomach wall in these animals are complex; the immense muscular pillars of the rumen are capable, as we have seen, of mixing, churning, and revolving the contents of the organ. That rotation occurs is certain from the formation of hair balls from material swallowed by the animal in licking its body, or, in the case of sheep, from wool torn out when scratching themselves and subsequently swallowed. The rumen and omasum are constantly at work, the rumen contracting a little oftener than three times a minute; the reticulum, on the other hand, has periods of rest, likewise the true stomach. In the latter the movements must be of a most simple character, as in the single stomach of other animals.

The movements of the stomach are excited by the presence of food, or by any irritation applied to the mucous membrane. These movements are rendered more energetic by stimulation of the vagus, but even when all the nerves going to the part are divided, the stomach can still contract, which is probably due to the ganglia contained in its walls. The stomach is, then, an automatic organ. Nevertheless, it is supplied by both pneumogastrics, the nerves being non-medullated; in addition, it obtains sympathetic fibres from the solar plexus, to which the right vagus also sends some fibres (see Fig. 80, p. 236). In the wall of the stomach ganglia are found with which both the vagus and sympathetic communicate. The vagus may be regarded as the motor nerve of the stomach, while the sympathetic is mainly inhibitory; stimulation of the vagus leads to contraction of the stomach walls, stimulation of the sympathetic causes dilatation of a contracted stomach and relaxation of the pylorus. The vagus supplies the bloodvessels with dilator fibres, whilst the sympathetic supplies them with constrictor fibres. Section of the vagus in the horse causes paralysis of the stomach. In other animals, if the movements are not abolished, they are certainly diminished. The result of stomach paralysis is that nothing passes on to the intestines, so that in the horse even large poisonous doses of strychnine may thus fail to cause death by lying inert in the stomach. This experiment demonstrates the uselessness of giving medicine by the mouth in many cases of digestive trouble in the horse; the material lies in the stomach owing to paralysis of the organ, and is not absorbed.

The *nervous supply of the stomach of ruminants* is derived mainly from the vagus, excepting in the case of the third compartment, which has a separate and, at present, unknown source of supply. Stimulation of the vagus was found by Ellenberger to produce energetic contraction of the reticulum, slow kneading movements of the rumen, and after an interval slower and peristaltic contractions of the abomasum, but no contraction of the omasum. Section of both vagi was found to cause paralysis of the œsophagus, rumen, and reticulum, followed by tympany of the rumen. Ellenberger could not obtain any effect on the stomach movements by stimulating the sympathetics.

The influence of the mind over stomach digestion is well known in man, and we have already noted its effect in the horse in the feeding experiment related on p. 186. Pavlov's fistula has enabled this point in the lower animals to be settled with accuracy. One of his dogs, while actively secreting gastric juice under the influence of a 'sham meal,' was made angry and excited by being restrained from chasing a cat; the gastric glands at once ceased secreting. Similarly by means of X rays the movements of the cat's stomach have been observed to cease when the animal became angry and excited.

SECTION 3.

Intestinal Digestion.

The chyme which is poured from the stomach into the small intestines meets there with three digestive fluids—viz., the succus entericus, the bile, and the pancreatic juice.

The **Succus Entericus** is prepared by the glands of the small intestines; the glands of Brunner are found in the duodenum, and the follicles of Lieberkühn throughout the whole of the small and large intestines. Lieberkühn's crypts supply a considerable proportion of the intestinal juice, while the secretion from the glands of Brunner is scanty. Brunner's glands, which are very large in the horse, are arranged on the same principle as the gastric glands, while those of Lieberkühn are tubular glands, amongst the cylindrical epithelial cells of which numerous mucus-forming goblet cells may be found.

The total daily amount of succus entericus secreted by the horse is given by Colin as 10 litres (17 pints).

At one time it was considered that the succus entericus was a comparatively unimportant fluid, the chief function of which was to neutralise the acid chyme; Colin, however, showed that in the horse it has a distinctly digestive effect. The Lieberkühn fluid is considerable in amount and alkaline in reaction owing to the presence of carbonate of soda. It is now known that though a pure secretion of Lieberkühn's crypts has little or no digestive action excepting on starch, an extract of the intestinal wall and juice squeezed from it have a most important function. The intestinal extract, on the other hand, contains three types of enzymes, and in addition a peculiar chemical substance of remarkable properties. The enzymes are:

1. **Enterokinase,** which converts the trypsinogen, the mother substance of the pancreatic proteolytic enzyme, into trypsin.

2. **Erepsin,** a proteolytic ferment, which supplements the work of trypsin, acting on deutero-albumoses and peptones, breaking them up into amino-acids and hexone bases.

3. **Inverting Ferments,** converting double sugars which cannot be utilised by the tissues into single sugars which can. Of inverting ferments there are three:

Maltase, converting maltose and dextrin into dextrose.

Invertase, converting cane sugar into dextrose and levulose.

Lactase, converting milk sugar into dextrose and galactose.

Finally, the intestinal fluid contains secretin, which is not a ferment, but a chemical substance (*hormone*) found in the walls of the small intestines; this, when taken into the blood, possesses the singular property of causing the secretion of pancreatic juice.

Enterokinase, erepsin, and secretin will be dealt with in considering the pancreas.

Intestinal Digestion in the Horse.

Immediately or shortly after the ingesta leave the stomach the contents are neutralised by the pancreatic and biliary secretions. So rapid is this change that on the duodenal side of the pylorus the reaction of the previously acid chyme is neutral, and a few inches along the duodenum it is alkaline; this alkaline reaction is at first faint, but becomes more marked as the ileum is approached. Ellenberger describes the contents of the small intestines as being acid in the first two-thirds of their length, then neutral as far as the ileum, where they become alkaline; we have only once found them other than alkaline throughout. He further states that in the fasting horse the contents are alkaline, but that in the digesting animal, whether horse, ox, or sheep, they are acid, the acidity decreasing after passing the common duct, and the contents becoming decidedly alkaline at the posterior portion of the small intestine. This, as has been said, does not agree with the writer's experience in the horse; it is usual to find the contents of the duodenum next the pylorus neutral, and from this point the bowel contents are faintly alkaline, the reaction increasing in intensity up to the ileum, where the contents are always markedly alkaline. We have only once found the small bowels acid in the horse, no matter what diet has been given, or at what period of digestion the examination has been made; a neutral or faintly alkaline reaction in the anterior part of their course, and marked alkalinity in the posterior portion, is doubtless the rule rather than the exception.

The arrangement of the small intestines suspended, or dangling in festoons from the spine, by a very delicate membrane is a construction the advantages of which are not very apparent. It appears to invite trouble. The long mesentery is considered to favour volvulus, but no doubt the chief cause of this trouble is tympany. If, after death, the bowels be artificially distended with air, loops of them behave in such a way as would lead to twist in the living animal.

Physical Characters of the Chyme.—The chyme having passed into the bowel, its appearance at once changes, for the acid albumin is precipitated by the alkaline secretion found there. It is now observed that the material consists of clots floating or suspended in a yellowish fluid, extremely slimy in nature and resembling in appearance, because of its precipitated albumin, nasal mucus suspended in fluid. The proportion of mucin must be considerable, judged from the ropiness of the fluid when poured from one vessel to another, and this mucus is probably derived largely from the stomach. Throughout the small intestines the character of the chyme is as follows—viz., a yellow, frothy, precipitated, slimy fluid, the material from the anterior part of the intestinal canal having a peculiar mawkish smell, while that from the region of the ileum has a distinctly fæcal odour; this is due to indol and skatol, formed during, or subsequent to, pancreatic digestion. In the ileum the proportion of fluid material is considerably reduced in amount, and what was previously almost impossible, the character of the ingesta may now be recognised.

Function of the Ileum.—As the flow of material into the small intestines is controlled by a sphincter, so is the flow out of them. The ileum is a remarkably thick and powerful bowel; it is always found contracted and containing material which is dry compared with that found in the anterior portion of the intestine. One of the functions of the ileum is to control the passage of material into the cæcum. Colin describes the chyme in the horse as circulating between the pylorus and ileum—that is to say, it is poured backwards and forwards in order to expose it sufficiently to the absorbent surface; this necessitates a reversed peristaltic action. He says that were it not for this arrangement the material could not be acted upon and the chyle absorbed, as the passage of fluid through the small intestines is very rapid. It would have been impossible to reason out that the fluid material of the small intestines was passed to and fro between the stomach and the ileum, exposed, as Colin expresses it, twenty times over to the absorbent surface of the bowels. This observation must have been made as the result of his examination of the living animal, and there can be no doubt of its correctness.

Experiment shows that water will pass from the stomach to the cæcum in from five to fifteen minutes. By applying the ear over the duodenum of a drinking horse, the water as it passes under the last rib on the right side may be heard rushing through the intestines on its way to the cæcum. One is always struck by the fact that the small intestines are never found full—in fact, are often practically empty—from which we judge either that material passes very rapidly through them, or that only small amounts of chyme are propelled into them at a time. The contents are always in a liquid condition excepting at the ileum, the fluid being derived from the secretions poured into and those originating in the bowel. That active absorption goes on in the intestines is proved by the differences in the physical characters of the contents of their several parts. The rate at which the chyme passes through the small intestines varies with the nature of the food, and the frequency with which the horse is fed. Ellenberger says it reaches the cæcum six hours after feeding, but has not entirely passed into this bowel for twelve or even twenty hours; we have known it reach the cæcum in four hours.

In the small intestines the chyme meets with the bile and pancreatic juice; the action of these will be described in the chapter dealing with the liver and pancreas. The absorption of chyle, and its elaboration before reaching the blood, are points which must be reserved for the chapter on 'Absorption.'

Large Intestines.

There can be no doubt that in solipeds digestion in the large intestines is a very important process; at least, we judge so from their enormous development. In many respects they present a considerable contrast to the small intestines; they are always found filled with ingesta, the contents are more solid, the material lies a considerable time in them, and no juices other than the succus entericus are poured into the bowel. These are conditions exactly the reverse of those found in the small intestines. The bowels which are spoken of as the large intestines are the cæcum, double and single colon, and the rectum.

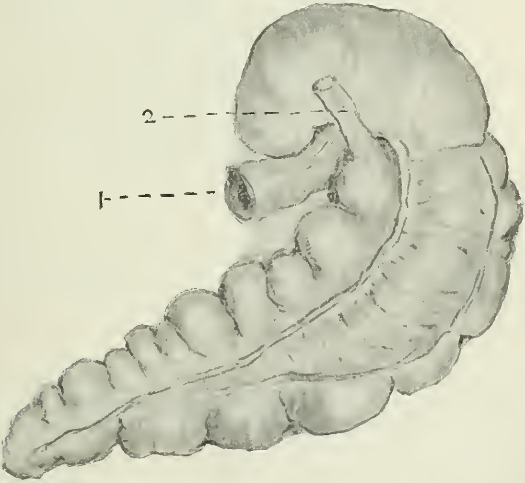

FIG. 73.—CÆCUM OF THE HORSE IN POSITION, ITS INNER FACE BEING SEEN.
1, The first colon; 2, the ileum.

The **Cæcum** has been described by Ellenberger as a second stomach; its enormous capacity and fantastic shape have always rendered it an intestine of considerable interest (Fig. 73). To our mind its most remarkable feature is that it is a bag, the openings into and out of which are both found in the upper part, close together; the exit, strange to say, is above the inlet, and the contents have to work against gravity in order to obtain an entry into the next intestine, the double colon. This is made possible by the four muscular bands on the cæcum (Fig. 74), which shorten the bowel, forcing the contents upwards towards the 'crook.' The ileum being closed, the only available outlet is into the colon (Fig. 75).

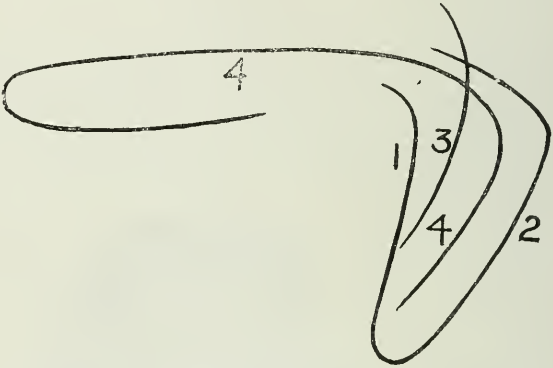

Fig. 74.—Schematic Arrangement of the Longitudinal Muscular Bands of the Cæcum.

Bands 1 and 2 are one, and form a complete sling for the bowel; band 4 runs from the cæcum to the pelvic flexure of the colon. It is a remarkable band, and doubtless intimately connected with the mechanism which brings about the passage of material from cæcum to colon. 3 is a single band belonging exclusively to the cæcum.

On the nature of the communication between the large and small intestines several questions suggest themselves. It would seem certain that in order to get from the ileum into the colon everything must pass into or, at any rate, through the cæcum, yet we feel sure that material does not remain there long. Is it possible that the openings of the ileum and of the colon might be brought together so that material may pass directly from one into the other? Nothing is returned into the ileum from the cæcum; there must, in consequence, be a sphincter keeping the ileum closed, for when the cæcum contracts material must cross the opening of the ileum in order to reach the colon (Fig. 75). This sphincter is furnished by the thickened condition of the wall of the ileum. We see no difficulty in believing that the rigid end of this tube may pass almost all its solid contents direct into the colon, and the slightly funnel-shaped arrangement of the latter would readily admit the rigid nozzle of the ileum.

The contents of the cæcum are always fluid, sometimes quite watery, occasionally of the colour and consistence of pea-soup, and when in this condition they are full of gas bubbles; when watery, the fluid is generally brownish in colour, with particles of ingesta floating about in it. The reaction of the contents is always alkaline; all observers are agreed on this point.*

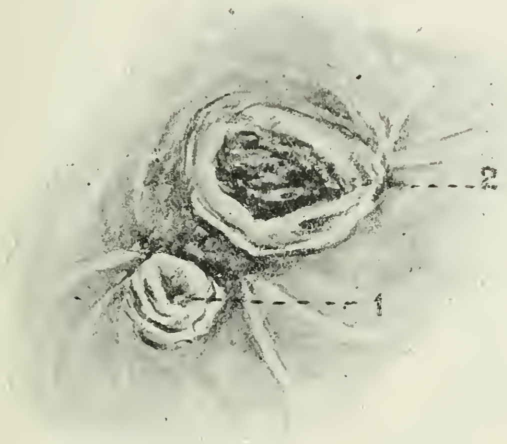

Fig. 75.—The Openings of the Ileum and Colon in the Cæcum.

1, The ileum; 2, the colon. In the figure the openings are represented close together, but even when stretched apart they are less than 4 inches distant.

The cæcum is most admirably arranged as a receptacle for fluids, and though absorption undoubtedly occurs from it, and digestion of cellulose takes place in it, yet we believe its chief function is the storing up of water for the wants of the body and the digestive requirements, as it is absolutely certain that digestion in the horse can be properly carried out only when the contents are kept in a fairly fluid condition. We do not say that the cæcum produces no digestive changes in the food, for we have stated that the contents are occasionally of the consistence of pea-soup, exhibiting active fermentation, but we consider its digestive function subordinate to its water-holding one. Ellenberger, on the other hand, views the cæcum as a bowel for the digestion of cellulose, where by churning, maceration, and decomposition, this substance is dissolved and rendered fit for absorption, and he likens it to the stomach of ruminants and the crop of birds. He further considers that the cæcum owes its existence to the small size of the stomach, and the rapidity with which the contents are sent along the small intestines. His experiments demonstrated that the entire 'feed' reaches the cæcum between twelve and twenty-four hours after entering the stomach, that it remains there twenty-four hours, and that during that time 10 to 30 per cent. of the cellulose disappears.

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* The writer only once found the cæcum acid.

The digestion of cellulose is no doubt a very important matter, especially as we know that the poorer the food the more cellulose digested; but we are not prepared to admit that food necessarily remains in the cæcum twenty-four hours, and we believe that cellulose digestion occurs principally, though not entirely, in the colon, and, further, that it is not absolutely necessary for the material to remain in the cæcum, but that it may pass on at once to the colon. The writer's experiments on digestion have shown that ingesta may reach the cæcum three to four hours after entering the mouth, and we are quite clear on the point that oats may travel some considerable distance along the colon in four hours from the time of being consumed, though we regard this as exceptionally rapid. For example, a horse which had never had maize and had not tasted oats for two or three years was fed first with 2½ pounds of maize, and seventeen hours later with 4 pounds of oats. The animal was destroyed four hours from the time of commencing to eat the oats. Much maize and a few oats were found in the pelvic flexure of the colon, and a certain proportion of maize and a quantity of oats in the stomach. In twenty-one hours the small ration of 2½ pounds of maize was distributed between the stomach and pelvic flexure of the colon, which is a very large area. In four hours the oats reached the same point in the bowel that the maize had arrived at; this is exceptionally rapid, but this experiment supports two points it is desired to emphasise—viz., the difficulty in getting the stomach to empty itself completely, and the rapid transit of material through the small intestines.

Colin believed that in the cæcum starch can be converted into sugar, fats emulsified, and that the active absorption of assimilable products occurs there.

The Colon.—The direction taken by the colon of the horse is remarkable. It commences high up under the spine on the right side, its origin being very narrow, but it immediately becomes of immense size; it descends towards the sternum, and, curving to the left side, rests on the ensiform cartilage and inferior abdominal wall. The colon now ascends towards the pelvis, and here makes a curve, the bowel becoming very narrow in calibre; the pelvic flexure having been formed, the intestine retraces its course towards its starting-point. Running on top of the portion previously described, it descends towards the diaphragm, growing gradually larger in calibre, and then ascends towards the loin, being here of immense volume—in fact, at its greatest diameter; it then suddenly contracts, and forms the single colon (see Figs. 76 and 77). The object of the variations in the volume of the double colon appears to be the convenience of its accommodation in the abdominal cavity.

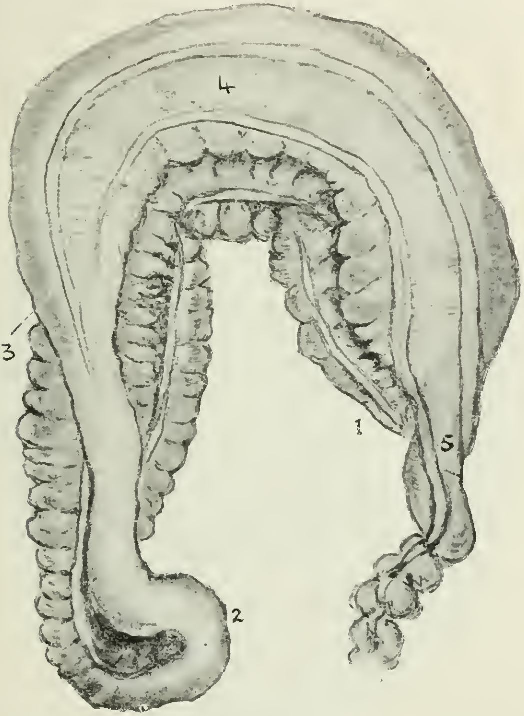

Fig. 76.—The Double Colon looked at from Above (modified from Müller).

1, The first colon, the cæcum removed; 2, the pelvic flexure, the bowel being narrow; 3, the colon suddenly enlarges; 4, its diaphragmatic flexure; 5, the single colon. Several of the bands are seen; note also the sacculated and non-sacculated portions of the bowels.

The double colon may, for the purpose of description, be divided into four portions: the ingesta in the first and third descend, in the second and fourth ascend. It is found that the physical characters of the contents are not the same throughout. In the *first colon* the food is fairly firm, and the particles of corn, etc., can be readily recognised; in the *second colon* the material is becoming more fluid, while at the *pelvic flexure* the contents are invariably in a liquid, pea-soup-like condition, and the particles of which they are composed are not readily recognised. In the *third colon* the material becomes firmer, but only slightly so, and bubbles of gas are being constantly given off from its surface; in the *fourth colon* the entire ingesta are like thick soup, and the material composing them is in a finely comminuted condition, the surface being covered with gas bubbles. For the first foot or so of the *single colon* this condition is maintained, when quite suddenly the contents are found solid and formed into balls. The remarkable suddenness of this change is invariable in a state of health, and indicates either most active absorption, or that the contents are subjected to great compression. The entire contents of the colon are yellow in colour or yellowish-green,

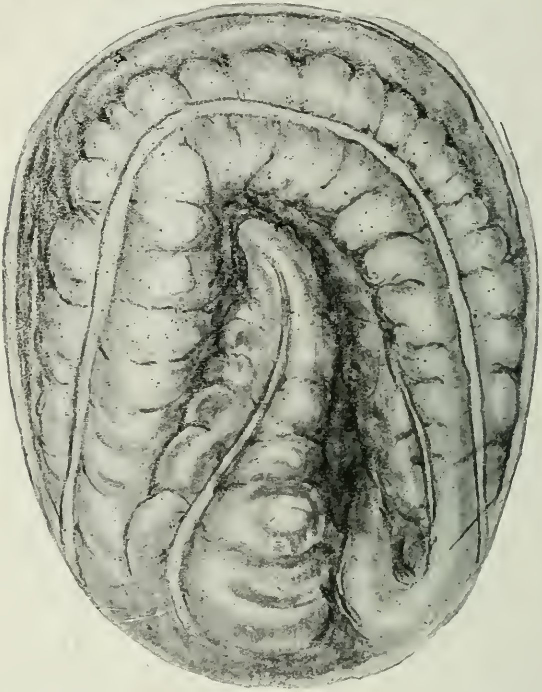

FIG. 77.—POSITION OF THE CÆCUM AND DOUBLE COLON ON THE FLOOR OF THE ABDOMEN SEEN FROM BELOW.

The point of the cæcum is directed towards the sternum. The abdomen has spread open in front owing to the needful dissection. It should be egg-shaped, the narrow end foremost.

becoming rapidly brown or olive-green on exposure to the air, the colouring being due to the chlorophyll of the food. The contents of the colon are normally alkaline throughout; we once, however, found them acid.

Digestive Changes.—Large Intestines.

The changes food undergoes in the large intestine have never excited the same interest as those effected in the small. The absence of any secretion from the large bowel other than the succus may help to account for this, and may also assist in explaining why the large bowels have been regarded as reservoirs for ingesta, rather than as active centres of digestion. As a matter of fact, the large intestines of the horse are actively employed in dealing with cellulose and its allies, not by means of any known enzyme peculiar to the body, but rather by the process of bacterial disintegration, the result of decomposition. It is known that organisms may hydrolyse cellulose, and render it soluble. In the case of oats, we mentioned (p. 199) that they probably furnish their own cellulose enzyme, but auto-provision of enzymes has not been proved for all vegetable material. The cellulose of hay, if utilised, can only be so after prolonged maceration in the large intestines and the subsequent attack of bacteria. By some it has been considered that the epithelial cells of the intestine are capable of dealing with cellulose, but on this point no definite statement can be made. There is good reason for the extensive preparations made for cellulose digestion in herbivora —viz., that the cellulose encloses the protein, starch, and fat of vegetable substances in a framework, and until this is broken down these substances cannot be acted upon. We know that considerable cellulose solution must occur before the material arrives at the large intestines, otherwise neither in the stomach nor small intestine could digestion be the important function it is. The digestion of protein, fat, and sugar is largely, though not entirely, effected in the stomach and small intestine, but there must be a certain amount of these substances so firmly locked up in their cellulose envelopes that they are not liberated until after prolonged maceration and digestion in the large intestines. We may, therefore, safely assume that protein, fat, starch, and cellulose are capable of being acted upon in the large intestines of the horse.

As the final result of cellulose digestion carbonic acid and marsh-gas are formed in equal volumes, and when produced in excessive amounts cause acute disease and suffering.* We have in our description of the large intestines drawn attention to the appearance of the contents of the cæcum and fourth portion of the double colon. The contents, on the surface of which gas bubbles are constantly breaking, were described as like pea-soup. It may well be that these two places are the active seats of the final transformation of cellulose, the cæcum dealing with that which has already been acted upon in the stomach and small intestines, and the fourth colon being concerned with the more refractory cellulose, which has required prolonged maceration in the large intestines before becoming capable of solution. This view is supported by the remarkably rapid change in the character of the contents in the single colon, the somewhat pea-soup likeness giving way, in the space of a few inches, to the appearance presented by ordinary normal fæces.

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* The chapter dealing with 'Nutrition' should be consulted for further information on cellulose and its digestion.

The large intestines cannot exist entirely for the solution of cellulose. There are other processes going on, chief of which is the bacterial attack on the unabsorbed protein products of the small intestines. The small intestine may be regarded as practically free from putrefactive processes; in fact, it is only towards the ileum that the unpleasant products of pancreatic digestion can be detected. In the large intestine, on the other hand, putrefactive processes are evident throughout; the bacteria are here engaged, among other things, in attacking the unabsorbed products of protein digestion, and reducing them to simpler end-products, such as proteoses, peptones, amino-acids, indol, skatol, phenol, phenyl-propionic, phenyl-acetic and fatty acids, with the evolution of CO_2, H_2, H_2S, and CH_4. The aromatic end-products are partly got rid of through the fæces, and partly absorbed into the blood, taken to the kidneys, and, combining with sulphuric acid, are got rid of through the urine; especially is this true of phenol, indol, and skatol.

Metschnikoff made a special study of the organisms living in the intestinal canal of man, and arrived at the conclusion that in the myriad population of the intestinal tract there are at least three anaerobic organisms which can produce very virulent poisons. These poisons, which are of the aromatic series, phenols and indols, are absorbed by the intestinal wall. Metschnikoff regarded the colon with grave suspicion, and believed that its defects are the cause of men not dying from old age. Diseases of the colon certainly cut short the useful life of many horses.

As the material moves towards the rectum it becomes drier and drier, and more thoroughly formed into balls by the action of the bowel-sacs, which squeeze the mass into a round or oval shape. The contents of this portion are still alkaline, or slightly so. As we approach the anus a distinctly acid reaction is obtained on the surface of the fæces, though at this time the interior of the ball may be, and often is, alkaline; the converse of this may also be observed. In the rectum the single balls collect in a mass, to be forced out of the body at the next evacuation. The reaction of this mass is acid, and its colour depends on the food, being, on an ordinary diet, of rather a reddish-yellow or brownish tint, due to altered chlorophyll.

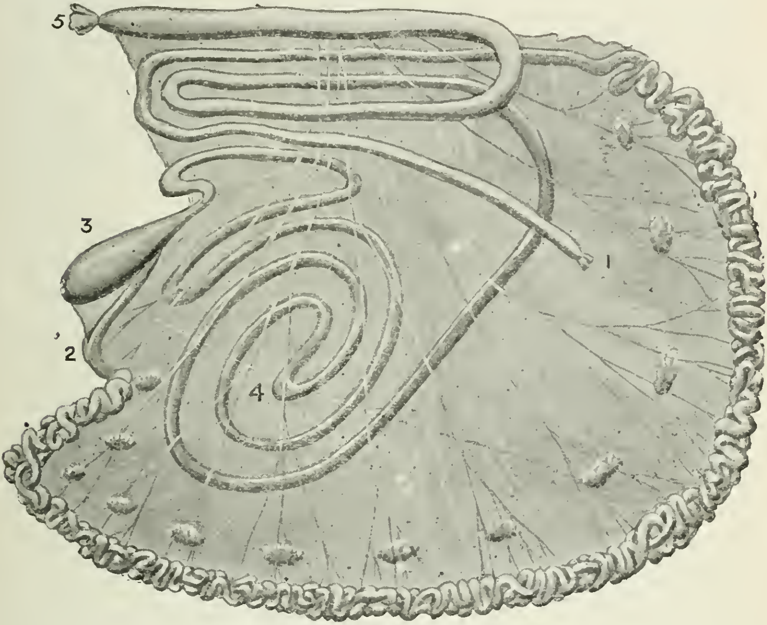

FIG. 78.—SCHEMATIC ARRANGEMENT OF THE INTESTINES OF THE OX.

1, The small intestines; 2, their termination in the cæcum; 3, the cæcum; 4, the 'spiral' colon; 5, the single colon. In the spiral colon it will be observed that the ingesta travel apparently in opposite directions.

There is undoubtedly absorption from the single colon and from the rectum. Animals may be killed by the rectal injection of strychnine; narcosis can be produced by the rectal administration of ether, and life may be supported, at any rate for a short time, by means of nutrient enemata. Absorption from the single colon and rectum is rapid; the marked change in the physical character of the fæces is evidence of this.

Intestinal Digestion in Ruminants.

Though intestinal digestion is so important in the horse, it would appear in ruminants to occupy a position subordinate to stomach digestion. It is curious why in one animal the changes should occur at the anterior, and in the other at the posterior part of the digestive tract, but this difference in the arrangements for digesting cellulose depends upon the one being capable of rumination and the other not. The rumen of the ox corresponds to the large intestines of the horse. The intestines of the ox are of extreme length, but small in calibre; they are half as long again as those of the horse, and it would appear that their chief function is that of absorption. Their arrangement, especially that of the large intestine, is most singular. The small intestines are hung in convolutions on a mesentery; they are narrow in diameter, and about 120 feet in length. The large intestines are about 9 metres (30 feet) in length, also narrow and without muscular bands or puckerings, as in the horse; the colon is arranged in a remarkable spiral manner between the folds of the mesentery (see Fig. 78).

It is in this immense length of absorbent surface that the food substances capable of being utilised are taken up. It is clear, however, that certain digestive changes occur in the small intestines, into which, as in other animals, the pancreatic and biliary fluids are poured. Here the proteins which have escaped the stomach, and the fats and starches, are changed and rendered fit for assimilation; the altered cellulose only finds its way here when rendered fit for absorption by its digestion in the rumen, that is, assuming any portion of it escapes being hydrolysed into carbon dioxide and water, see p. 201.

Intestinal Digestion in other Animals.

In the pig intestinal digestion is said to be of short duration, and absorption very rapid. **In the dog** the material passes out of the stomach slowly, and only in small quantities, into the small intestines, which are usually found collapsed. It is in the small intestines of this animal that the chief digestion occurs, as the large bowels are rudimentary. In the sheep, ox, pig, and dog, the reaction of the contents of the small intestines is acid anteriorly and alkaline towards the ileum; probably in all animals the contents of the large intestines, unless in the rectum, are alkaline in reaction.

The following table gives some information regarding the intestinal canal in the domestic animals, which helps to explain some of the differences in their modes of digestion.

The intestinal capacity is, on an average:—

Horse - - - -	200 litres—	44 gallons.
Ox - - - -	80 ,,	17·5 ,,
Pig - - - -	27 ,,	5·9 ,,
Dog - - - -	8 ,,	1·75 ,,

Ratio of length of intestine to length of body:

Sheep	26 times longer.
Ox	20 ,, ,,
Horse	12 ,, ,,
Dog	5 ,, ,,

Movements of the Intestines.

The movements of the intestines are brought about by the involuntary muscle composing the wall. This muscle in the small intestines is arranged in two layers, one circular, the other longitudinal, while in the large intestines narrow bands of pale muscle of considerable length take the place of the ordinary longitudinal layer, and may be found on all parts where the tube is sacculated. In fact, one function of the bands is to bring about the sacculated condition of the canal, an important arrangement whereby economy of space is effected with no loss of surface.

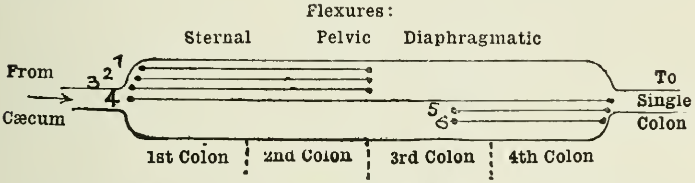

Fig. 79.—Schematic Arrangement of the Muscular Bands on the Double Colon.

The colon is supposed to be opened out into a straight tube. Bands 1, 2, and 3 run from the first colon to the pelvic flexure; one of the three actually comes from the apex of the cæcum. No. 4 is the only band running the whole length of the bowel. Nos. 5 and 6 originate in the region of the third colon and finally run to the single colon.

The sacculated condition of the double colon in the horse is confined principally to the first, second, and fourth portions. The third portion, especially at the pelvic flexure, is free from sacculations, and the fourth portion is not so liberally puckered as the first and second. On the first colon there are four bands, on the second colon there are also four, three of which disappear at the pelvic flexure; on the third portion there is only one band, while on the fourth colon there are three (see Figs. 74 and 79). In the large intestines the longitudinal layer of fibres is confined to the muscular bands, so that the greater portion of the wall consists of circular muscle only. The longitudinal bands shorten the bowel, but the work of pressing the contents along is performed by the circular layer. The bands, in fact, are numerous where the intestine is large, and reduced in number where the bowel becomes smaller. This arrangement suggests that they may, under suitable conditions, produce an irregularity of pull, and we can see no other explanation of displacement of the large intestines of the horse (a matter dealt with more fully at the end of this chapter) than such action of these muscular bands.

The muscular movements of the large intestine are slower than those of the small bowels; possibly one reason for this may be that the food has to remain a longer time in contact with the absorbing surface—viz., for at least forty-eight hours, and usually for as long as four days. The peristaltic movement of the small intestines is quite distinct from that of the large; the one movement ends at the ileum, the other begins at the cæcum.

The muscle of the intestinal wall causes the movement known as **peristalsis,** which normally passes in the direction stomach to rectum. Relatively quick in the small intestines, it becomes slower and more deliberate in the large, but the wave has always this one object in view—viz., to press the ingesta onward. A wave of contraction passing the reverse way—viz., in the direction of rectum to stomach—is known as **antiperistaltic:** such a movement is considered abnormal, but in the horse, according to the observations of Colin, antiperistalsis of the small intestines is a natural condition. Some physiologists recognise antiperistaltic movements of the large intestines as being normal in certain animals, producing a to-and-fro movement of the contents, but it is generally thought that in the small bowels antiperistalsis is present only under abnormal circumstances. If antiperistalsis be admitted for the large bowels, we see no difficulty in its extending to the small, especially in view of Colin's positive statement that it occurs. The peristaltic wave depends upon a something peculiar to the bowel wall, for if a piece of small intestine be experimentally reversed, so that the portion originally near the stomach is made to occupy the position farther away from it, it is found that the peristaltic wave in the reversed segment is still in the original direction instead of in the new direction. The actual mechanism involved in a peristaltic contraction, according to Starling and Bayliss, is as follows: The circular muscle on the stomach side of the bolus contracts, while that on the far side is relaxed for some distance, so that the advancing wave drives the bolus into a relaxed portion of bowel. If a solution of cocaine or nicotine be applied to the intestinal wall these movements cease, from which it is argued that they are probably due to local ganglia.

Rhythmical or **Pendular** movements of the small intestines were first described by Starling and Bayliss. They consist of a series of local contractions caused by the presence of food in the canal, and occur in the dog at the rate of twelve, and in the cat of thirty times a minute approximately. They have been studied by means of the Röntgen rays and a bismuth diet. Pendular movements are essentially connected with the division and subdivision of food in the intestinal canal; by means of the rays a string of material may be seen to become suddenly segmented, each segment again dividing, and each of these may in turn be further subdivided in a perfectly definite manner. In this condition each segmented portion is exposed to thorough mixing with the secretions in the intestine, and to enable the finely divided contents to be so acted upon the bowel is for a time free from peristalsis. After this interval, a peristalsis sweeps together all the scattered atoms, and forms them once more into a string of material. This remarkable pendular movement is unaffected by the action of cocaine or nicotine, which has been shown to inhibit at once the ordinary peristaltic movements.

In the dog, in addition to peristaltic and pendular movements, another movement has been described much slower, but also rhythmical, which may be carried out for twenty or thirty minutes at intervals of two hours, even when the canal is empty.

We have been told by Colin that digestion in the small intestines of the horse is carried on by peristalsis and antiperistalsis, the fluid travelling from stomach to ileum, and from the ileum towards the stomach. Pendular movements are of no value in the small intestine of this animal, for as, until the ileum is reached, the entire material is fluid, there are no strings of food to be segmented. This may account for pendular movements of the bowels not having been observed in the horse.

In the first and third portions of the colon of the horse the ingesta travel by their own gravity; in the second and fourth portions they travel against gravity, as in the cæcum. As the first and fourth and second and third portions of the colon are united, the curious result follows that material is passing along each section in two apparently opposite directions.

The frequency of intestinal affections in the horse causes the canal to be of exceptional practical interest. When the cæcum is found completely inverted into the colon, as if a hand had passed through the colo-cæcal opening, laid hold of the apex of the cæcum, and drawn the entire bowel within the first portion of the colon, it is then that the question of muscular movements so strongly presents itself; or, again, when what is far commoner and equally fatal occurs—viz., displacement or actual twist of the large bowel, or a complete twist of the small intestine, leaving the bowels in such indescribable complexity that the parts cannot be unravelled, even when removed from the body; or, finally, in a condition rare in the horse, probably in all animals, but still well recognised, in which telescoping of the small bowels occurs, known as 'intussusception.' It is impossible to believe that muscular action of the intestines is free from all blame in the production of these conditions. It is easier to understand a twist of the small intestine apart from muscular action than it is to understand displacement or actual twist of the large intestine. A loop or coil of small intestine may be so distended by gas or by ingesta as to become twisted, but it is more difficult to imagine either of these producing twist or displacement of the large intestines, and it becomes a question, as we have previously said, of how far the action of the muscular bands of the bowel may have a contributing influence. That great force is necessary we cannot doubt, bearing in mind the difficulty, if not impossibility, of restoring the parts to their original positions post mortem, or reproducing the lesions experimentally after death. These matters will be referred to again.

Nervous Mechanism of the Intestinal Canal.—Two distinct impulses are conveyed by the intestinal nerves—viz., to contraction and to inhibition. In the anterior part of the tract the former function is mainly or entirely carried out by the vagus, stimulation of which is found to cause active contraction of the small intestines. Contraction of the large intestines is effected through branches of nerves which issue from the sacral portion of the cord, and pass with the nervi erigentes to the hypogastric plexus. From this plexus fibres run to the large intestines, which produce on stimulation much the same results as stimulation of the vagus—viz., active contraction of both circular and longitudinal coats.

Stimulation of certain branches of the sympathetic nerve stops or inhibits the contractions produced by stimulation of the vagus, hence the term 'inhibitory.' The inhibitory nerves of the small intestine are derived from the dorso-lumbar portion of the cord, pass by the rami communicantes (*rc.*, Fig. 80) to the main sympathetic chain, *Sy.*, and thence through the large and small splanchnic nerves to the solar plexus, from which the final distribution to the intestines is made. The inhibitory fibres for the large intestines are derived mainly from the lumbar cord through *rc.* and *Sy.* (Fig. 80), and pass through to the inferior mesenteric ganglion. From this ganglion inhibitory fibres are supplied to both longitudinal and circular coats. The connections of the abdominal sympathetic ganglia of the horse are shown in Fig. 81.

Contractions of the bowels and peristalsis can occur after all nerves leading to the intestines have been divided; this points to the existence of local ganglia, and such may yet be found in the intestinal wall. The intestinal movements are automatic and self-regulated, though they can be provoked by both chemical and mechanical stimuli. The normal stimulus to peristalsis is

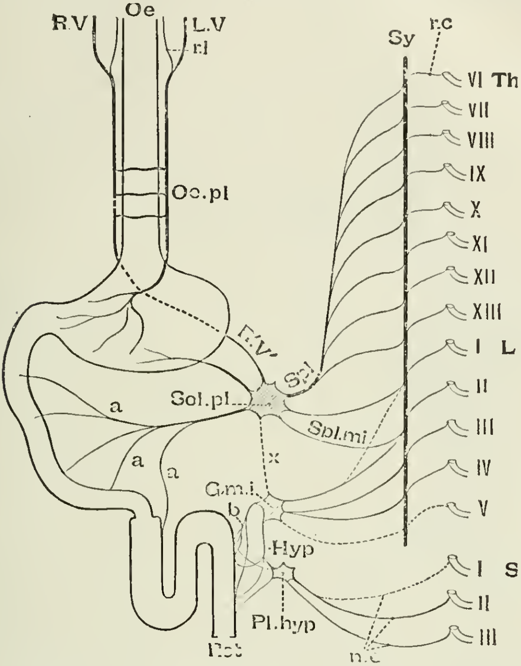

FIG. 80.—DIAGRAM TO ILLUSTRATE THE NERVES OF THE ALIMENTARY CANAL OF THE DOG (FOSTER).

(The figure is very diagrammatic, and does not represent the anatomical relations.)

Oc. to *Rct.*, The alimentary canal from the œsophagus to the rectum.

LV., Left vagus nerve ending on the front of the stomach; *r.l.*, recurrent laryngeal supplying upper part of œsophagus; *R.V.*, right vagus joining left vagus, in the œsophageal plexus, *Oe.pl.*, supplying the posterior part of the stomach continued as *R'V'.* to join the solar plexus, *Sol. pl.*, *here represented by a single ganglion*, and connected through *x* with the inferior mesenteric ganglion (or plexus). *a*, *a*, *a*, branches from the solar plexus to stomach and small intestines, and *G.m.i. b*, from the mesenteric ganglion to the large intestines.

Spl., Large splanchnic nerve arising from the thoracic ganglia of the sympathetic, *Sy.*, and rami communicantes, *r.c.*, of the dorsal nerves.

Spl.mi., Small splanchnic nerve. Both the large and small splanchnics join the solar plexus, and thence make their way to the alimentary canal, supplying the small intestine with inhibitory impulses.

G.m.i., Inferior mesenteric ganglion formed by nerves running from the dorsal and lumbar cord. From this ganglion inhibitory nerves are given off to the large intestines.

n.e., Nervi erigentes arising from the sacral cord, and proceeding to the hypogastric plexus, *Pl. hyp.* From this plexus impulses of a motor kind are supplied to the large intestines.

the passage of ingesta along the canal. In the dog, even the sight of food is said to promote peristalsis. Gases, such as CO_2, H_2S, and CH_4, and organic acids, such as acetic, propionic, caprylic, etc., act as stimuli, and promote contraction. This is a fortunate circumstance, as they are normal to the bowel in consequence of bacterial activity. Oxygen gas, on the other hand, inhibits movements, and, as a matter of fact, we know that oxygen gas does not normally exist, or exists only in traces, in the gaseous contents of the bowels. Cutting off the blood-supply to the bowels causes violent contractions, which occur again when the circulation is re-established; the former point is of interest in those cases of twist where the blood-supply is wholly or partly interfered with.

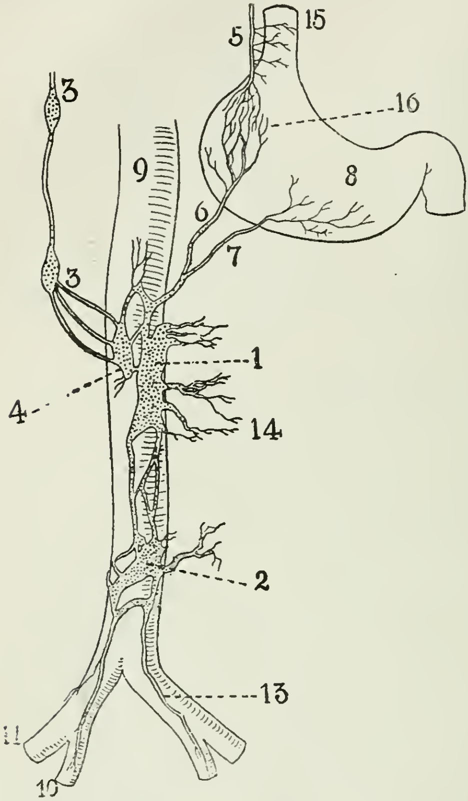

Fig. 81.—Abdominal Pre-Vertebral Sympathetic System of the Horse (Diagrammatic).

1, Anterior mesenteric ganglion; 2, posterior mesenteric ganglion; 3, sympathetic cord under the arches of the ribs; 4, the splanchnic; 5, the vagus passing to the stomach; 6, fibres from the anterior mesenteric ganglion joining the vagus; 7, branches of the sympathetic passing to the stomach; 8, the stomach; 9, the posterior aorta; 10, the internal iliac artery; 11, the external iliac; 13, pelvic branches of sympathetic; 14, mesenteric branches of sympathetic; 15, the œsophagus; 16, rich plexus formed by vagus and sympathetic nerves.

Under normal conditions the mind is not conscious of peristaltic movements, but when these become very energetic pain arises Under the influence of nervous excitement rapid and frequent evacuations of the bowels may take place in both cattle and horses. So rapid may the evacuations be that in the horse, in a short time, the whole of the rectum and single colon may be unloaded, Ordinary exercise is always an important cause of peristalsis. and a main factor in keeping the posterior bowels emptied.

As previously remarked, the normal stimulus to peristalsis is the presence of ingesta in the canal. In the feeding of herbivora bulk is essential; they cannot live in a state of health on concentrated food alone. Their intestines need bulky food, if only in order to maintain peristalsis. Bunge has shown that if cellulose be withheld from the diet of rabbits, they die from intestinal obstruction. It is the cellulose and lignin in the diet of herbivora which largely provide the needful stimulus to peristalsis.

Regulation of the Digestive Processes.—Under normal conditions, excepting that caused by hot fluids, there is no sensation in the alimentary tract posterior to the fauces; speaking generally, once the food has passed the point mentioned, we are no longer conscious of its existence. The intestines and stomach may be handled without causing pain. Nevertheless, in disease, when they are inflamed, tightly contracted, nipped, or immensely distended, the pain produced is acute, and, judging from the violence shown by horses, intolerable.

With the absence or apparent absence of an afferent nerve-supply, it is remarkable in what way the gastro-intestinal tract continues to discharge its supreme functions. There are no impulses passing to the brain or to the medulla directing operations, and it can be shown, experimentally, that extirpation of the abdominal sympathetic in the dog does not cause any interference with digestion, nor with the movements of the intestines. In fact, as we have just seen, movements of the intestines occur after all the nerves have been divided. It is more than likely that the key to the difficult problem is that furnished by Bayliss and Starling, and that the regulation of the gastro-intestinal tract is a chemical regulation by means of *hormones*. The existence of these substances has already been mentioned, and more will be said of their nature later, but it is well here to emphasise the fact that they are capable of acting after all nervous connections have been severed. They act through the medium of the blood.

Gases of the Intestines.—The largest amounts of gas found in the intestinal canal are in the cæcum and colon; the small intestines naturally contain very little, frequently none, whatever is formed there being probably rapidly passed into the large bowels. In the large intestines marsh-gas commonly exists, forming with carbonic acid the greater part of the gases present. The pathological conditions arising in the large bowels of horses, and in the rumen of cattle, as the result of fermentation—particularly of green food—and the enormous size to which these organs may in consequence be distended, are matters of common clinical experience. In both horse and ox the gas may generally be ignited a short distance away from the cannula which has been passed to give relief, the marsh-gas igniting readily on meeting with the proper proportion of oxygen. The whole of the chemical changes in the intestinal canal are carried out in the absence of oxygen; the gases which are produced depend mainly on the nature of the food, green material producing marsh-gas and carbonic acid, leguminous material producing sulphuretted hydrogen and hydrogen

For **Intestinal Absorption,** see p. 286.

The Fæces.—The fæces consist of that portion of the food which is indigestible, together with that part which, though digestible, has escaped absorption; mixed with these are water, colouring substances, mucin, organic matters in great variety, inorganic salts, bile pigment, volatile fatty acids, remains of digestive fluids, organisms, etc.

The composition of the fæces depends largely on the diet. The following table from Gamgee* is intended to give only a general idea of its composition:

APPROXIMATE COMPOSITION OF THE FÆCES OF THE HORSE, COW, SHEEP, AND PIG.

	Horse.	Cow.	Sheep.	Pig.
Water - - - -	76·0	84·0	58·0	80·0
Organic matter - -	21·0	13·6	36·0	17·0
Mineral matter - - -	3·0	2·4	6·0	3·0
	100·0	100·0	100·0	100·0

Considerable differences exist amongst animals in the consistency of the fæces; they are moderately firm in the horse, pultaceous in the ox, and hard in the sheep. These differences depend upon the amount of fluid they contain. In the pig they resemble human fæces and are very offensive; in the dog they are soft or hard, dark or light, according to the diet, the mineral matter of bones producing the light-coloured excreta. It is necessary to remember that the proportion of fluid in the fæces does not depend upon the amount of water which is drunk, but rather on the character of the food, the activity of intestinal peristalsis, and the energy with which absorption is carried on in the digestive canal. Succulent green food in horses produces a liquid or pultaceous motion; other foods, such as hay and chaff, have a constipating effect, the fæces being large and firm; excess of nitrogenous matter in the food produces extreme fœtor of the dejecta, and frequently diarrhœa, probably owing to putrefactive processes. Nervous excitement in horses frequently induces a free action of the bowels, accompanied by liquid fæces.

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* 'Our Domestic Animals in Health and Disease,' p. 253.

Fæces always float in water so long as cohesion is maintained. The colour of the fæces in the horse is yellowish or brownish-red, in the ox greenish-brown; they rapidly become darker on exposure to the air. When the animal is grass-fed the fæces are green, and when a horse is fed wholly on corn they become very yellow, and like wet bran in appearance. The colour of the fæces of animals receiving hay or grass is due to altered chlorophyll. The fæces of the horse are moulded into balls in the single colon. They are always acid in reaction, the acidity probably depending upon the development of some acid from the carbohydrates of the food.

Fæces contain, amongst the indigestible portion of the ingesta, lignin, a proportion of cellulose, husks of grains, the downy hair found on the kernel of oats, vegetable tubes and spirals, starch and fat granules, gums, resins, chlorophyll, etc.; unabsorbed protein, carbohydrate and fatty matters; products of digestive fermentation, such as lactic, malic, butyric, succinic, acetic, and formic acids; leucine, tyrosine, indol, skatol, and phenol; biliary matters and altered bile pigment—stercobilin—which gives the colour to the dejecta in the dog, but not in herbivora; and, lastly, mineral matter in varying proportions. In the dog, if fed on flesh, portions of muscle fibre, fat-cells, tendinous and fibrous tissue, are found in the fæces.

Of the *inorganic matter*, silica exists in herbivora in the largest amounts, then potassium and phosphates; sodium, calcium, magnesium, and sulphates, form a smaller but still important proportion. The horse excretes but little phosphoric acid by the kidneys, but considerable quantities pass with the fæces in the form of ammonio-magnesium phosphate. This salt is derived principally from the oats and bran of the food. In conjunction with calcium carbonate it frequently forms *calculi* through collecting in the colon around a pebble or nail as a nucleus. Other intestinal calculi are formed from collections of the fine hairs from the kernels of oats becoming encrusted with ammonio-magnesium phosphate, and forming oat-hair calculi. In the Persian wild goat and in certain antelopes intestinal concretions are found, known as Bezoar stones, formerly much used in medicine, and as antidotes to poison. There are two varieties of these calculi, one olive-green, the other blackish-green. The first melts when heated, emits aromatic fumes, and consists chiefly of an acid allied to cholalic acid. The chief constituent of the second variety is an acid derivative of tannic acid, which indicates the origin of these calculi from food substances. Stomach calculi have not been unknown in the horse, while in cattle, 'hair balls,' formed as the result of licking each other, are frequently found.

The following table by Roger gives the mineral composition of the fæces in every 100 parts of the ash:*

	Horse.	Ox.	Sheep.
Sodium chloride - - -	0·03	0·23	0·14
Potassium - - - -	11·30	2·91	8·32
Sodium - - - - -	1·98	0·98	3·28
Lime - - - - -	4·63	5·71	18·15
Magnesium - - - -	3·84	11·47	5·45
Oxide of iron - - - -	1·44	5·22	2·10
Phosphoric acid - - -	10·22	8·47	9·10
Sulphuric acid - - - -	1·83	1·77	2·69
Silica - - - - -	62·40	62·54	50·11
Oxide of magnesium - -	2·13	—	—

The **amount of fæces produced** in twenty-four hours varies with the quantity and nature of the food given. We have observed that on a diet consisting of 6 kilogrammes (13·2 pounds) of hay, 3 kilogrammes (6·6 pounds) of oats, and 1½ kilogrammes (3·3 pounds) of bran, the average amount of fæces passed by fifteen horses during an experiment lasting seven days amounted to 14 kilogrammes (30·8 pounds) in twenty-four hours, the fæces being weighed in their natural condition—viz., containing 76 per cent. water; the dry material of this bulk of fæces is about 3·25 kilogrammes (7·5 pounds). More fæces are passed during the night than during the day; in the above experiment, during the twelve hours, 6 p.m. to 6 a.m., the average amount passed per horse was 9 kilogrammes (19·8 pounds), while from 6 a.m. to 6 p.m. the amount was 5·5 kilogrammes (12·1 pounds). The largest amount of fæces we have known a horse produce was an average for many days of 33·3 kilogrammes (73·2 pounds), weighed in their natural state, in twenty-four hours; the diet consisted of 6 kilogrammes (13·2 pounds of oats, 1·5 kilogrammes (3·3 pounds) of bran, and 12·8 kilogrammes (28·15 pounds) of hay. In an experiment carried on for several months with different horses, each receiving 6 kilogrammes (13·2 pounds) of hay, and varying proportions of bran and oats, the average daily amount of fæces was 12 kilogrammes (26·4 pounds). A horse will evacuate the contents of the rectum about ten or twelve times in the twenty-four hours, and the food he consumes takes on an average four days to pass through the body.

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* Quoted by Ellenberger.

In the ox the amount of fæces is between 32 kilogrammes (70·4 pounds) and 37 kilogrammes (81·4 pounds) in the twenty-four hours. In the sheep it varies from 1 to 3 kilogrammes (2·2 to 6·6 pounds); in swine 1½ to 3 kilogrammes (3·3 to 6·6 pounds), depending on the nature of the diet.

The **odour of fæces** is distinctly unpleasant, owing to the presence of indol and skatol; in disease it is often extremely fœtid, and occasionally horrible.

The act of **defæcation** is performed by a contraction of the rectum, assisted by the abdominal muscles, the glottis being closed. In the horse contraction of the rectum alone is sufficient to expel its contents; this is proved by the fact that this animal can defæcate while trotting, showing there is no necessity to fix the diaphragm and hold the breath, though when at rest this does occur. It will thus be seen that the rectum of the horse can exercise extraordinary power; the hand and arm may be rendered almost numb by the pressure it can exert. The mass driven backwards by this force causes the sphincters to dilate, sometimes to an astonishing degree, and as the last trace of material is extruded, the contraction of the rectum is so great that it forces to the exterior some of the mucous membrane, which may be temporarily imprisoned by the contracting sphincters. The muscle of the rectum receives both motor and inhibitory fibres, as previously described. The extraordinary power of the muscle in the rectum of the horse may partly be due to the horizontal position of the body; there is no crouching of the body during the act of defæcation, such as occurs, more or less, in all other domesticated animals. The rectum has the whole work to perform without aid, even, as we have just shown, without the assistance of the diaphragm or abdominal muscles.

Two sphincters close the rectum in all animals—an external of voluntary and an internal of involuntary muscle; they are presided over by a centre in the cord. If this is destroyed, the rectum remains uncontracted, unable to empty itself, and the sphincter flabby; in the dog the cord may be destroyed in the lumbar region without interfering with the act of defæcation, which is then carried on by a reflex mechanism.

Meconium is the dark green material found in the intestines of the fœtus. It consists of biliary acids and pigments, fatty acids and cholesterin, while salts of magnesium and calcium, phosphates and sulphates, sodium chloride, soda, and potash are also found in it. Meconium is the product of liver excretion.

Pathological.

The internal diseases of early life in the horse are mainly of the chest, while those of the adult period are almost entirely confined to the abdominal viscera, principally the intestines. The term 'colic' appears to be indissolubly associated with the horse, and it becomes a question of the greatest practical and physiological interest to ascertain the reason why digestive disturbances are so common and so frequently fatal. There are certain obvious explanations of the fact, but neither separately nor in combination are the accepted ideas capable of explaining some of the mysteries surrounding the origin of these diseases.

When muscular spasms of the intestines occur, the disease is spoken of as **colic**. In many cases the pain which is exhibited is in no respect due to muscular spasm, and is only a symptom. Still, much the greater number of intestinal cases are of this kind—viz., simple muscular spasms of some part of the digestive tract, but of which part we are usually ignorant. It is obvious that the stomach, the small or the large bowels, may be so affected, but there are no definite symptoms which enable a positive diagnosis of location to be established. It is important to bear in mind the possibility of spasm of the muscular walls of the stomach, for there can be no doubt this is generally overlooked, and the intestines almost universally blamed. The evidence supporting the view we take of the liability of the stomach to disorder, is afforded by the frequency of rupture of this organ; not that the rupture is due to spasm of the walls, but that the spasm is caused by stomach trouble, the rupture following as a sequel, as detailed on p. 182. It is, however, admitted that stomach spasm is far less common than spasm of the intestinal portion of the tract. We would here emphasise the facts set forth on p. 209—viz., the general inability of the horse to vomit, and the serious bar this proves to relief; so much so, that it is hardly going too far to say that if the animal could vomit, ruptured stomach would be practically unknown, and stomach trouble generally a matter of comparatively slight importance. The bursting strain of the stomach is between four and five pounds on the square inch; when removed from the body and distended, it may rupture when the pressure is one-fourth or one-fifth of the above.

In connection with intestinal trouble, we are unable to say what proportion the cases in which the small intestines are affected bear to those in which the large are at fault. We cannot distinguish colic of the one from colic of the other during life. Still, there are good grounds for thinking that the large bowels are more frequently affected than the small—viz:

1. Ingesta pass rapidly through the small intestines—so rapidly, indeed, that, as mentioned at p. 220, these bowels are nearly always found empty at ordinary post-mortem examinations, or the contents in such a fluid condition that it is not reasonable to suppose, from what we know of the behaviour of fluids generally in the anterior part of the digestive tract, that they remain there long.

2. On the other hand, the large intestines always contain ingesta, for the material passes along them very slowly, so that, of the three or four days occupied in accomplishing the journey from mouth to anus, all but a few hours are spent in the large intestines. It is reasonable, therefore, to assume that in cases of purely uncompli-

cated disordered muscular action of the bowels, the large intestine in the majority of cases is at fault.

Colic is not fatal, though Percival described a fatal case. The writer's experience leads him to believe that death from simple spasm of the bowels is unknown, and he would emphasise the point, not only for the sake of accuracy, but as of value in prognosis. He believes that in the case of any horse returned as dying from colic, a more extensive search would have revealed some fatal lesion. There is no reason for believing that the pain of colic *per se* is capable of causing death.

If this be accepted—and it is fortunately capable of proof—it considerably narrows the causes of death from intestinal affections, and groups them mainly under two heads: (*a*) Inflammation of the bowels, and (*b*) displacement of the bowels.

Enteritis, by which name inflammation of the bowels is known, is spoken of as a common disease of the horse, but here again we join issue with accepted doctrines, and urge that it is an uncommon disease; further, that in the large majority of so-called cases of enteritis, some displacement of the bowels with interference to the circulation has occurred. That uncomplicated enteritis may exist is not disputed, but we urge its relative infrequency, and press the point that what looks like inflammation is more often strangulation. When a deep purple, thickened coil of intestine is found on opening the abdomen, such a case is not enteritis. The colour indicates that the blood-supply has been imprisoned as the result of strangulation, and an identical appearance would have been obtained by ligaturing the bowel. When half the double colon is found purple, thickened, filled with blood-stained fluid ingesta, the wall of the bowel being friable and its mucous membrane purple, then, however much we may be tempted to speak of it as enteritis, it certainly is not this disease, but strangulation. The term enteritis must be reserved for that condition of bowel in which the mucous membrane alone is inflamed. Such a bowel may give no external indication of trouble; the general vascular supply is not interfered with; the full intensity of the trouble falls on the mucous membrane, and such a condition may be experimentally produced by the administration of an irritant poison. It is probable that in the horse the majority, if not all the cases, of pure enteritis met with, are due to a poison produced during the process of digestive metabolism (see p. 228). That the presence of an irritant without a poison has no such effect is abundantly proved by the pounds of sand, gravel, and calculi horses may carry in their intestines for months, perhaps years, without producing any apparent ill effect, certainly without producing enteritis. Similarly, gastritis, excepting as the result of poison, is practically unknown.

Our object in the above remarks is to focus attention on defects in clinical observation, and to attempt a physiological analysis of the most frequent, the most fatal, and by far the most acutely painful and distressing group of diseases that any animal is exposed to. There is nothing in the whole range of comparative pathology, including the diseases of man, which compares in violence, suddenness, and mortality with the digestive diseases of the horse. We have attempted to show how physiology is capable of enabling us to steer a moderately accurate course, for it is certain that unless we are agreed regarding the nature of the lesions found at post-mortem examinations, we cannot reach that knowledge, the attaining of which is the object of our existence as a profession, and to which physiology is only the guide.

What is the most common cause of death among horses from intestinal affections, whether affecting the large or small bowels? There is only one answer to this, and time and careful inquiry will prove its accuracy. The answer is **Strangulation** of the bowels, partial or complete. This strangulation is capable of physiological analysis. The most unobservant person cannot overlook a bunch of small intestines so tied together as to defy all attempts at unravelling, even when out of the body, but it takes no little careful observation to detect displacements of the large intestine. The size, weight, and peculiar disposition of the double colon should secure it immunity from any form of displacement; when we look at the bowels in the abdomen, it appears impossible for any force, other than some mysterious power, to be able to influence their position, yet we know they are capable of being twisted as easily as if they were made of cotton. We know also that one portion may be thrust into another, in just the same way as a telescope collapses, constituting **Intussusception** and it is even possible for a voluminous bowel like the cæcum to become completely inverted, and found within the colon, though to get there it has to pass through an opening only an inch or two in diameter. So remarkable, indeed, are these lesions that they cannot always be imitated post mortem, and, as mentioned above, it is impossible to untie many complicated knots in the small bowels, even when the organs have been removed from the abdomen.

The actual mechanism which brings about twists of the large and small intestines is disordered muscular action; the factor responsible for telescoping intestines is disordered muscular action, and disordered muscular action is the result of disordered nervous action. For telescoping to occur, one portion of bowel must first contract until it becomes but a mere shadow of its former self; the contracted part must then be drawn within the dilated. A different cause is at work to produce a twist of the small intestine; this, as we previously indicated (p. 219) is tympany of the bowel, while in the case of the large intestines the muscular action must be capable of causing the bowel to perform a revolution more or less complete, and in this way reverse its position. We cannot attempt to indicate the exact disordered action which occurs; this problem would require to be worked out in the living subject. The colon and cæcum are most liberally supplied with bands (Figs. 73, 74, 76, 77, and 79), and it does not appear to us to be beyond the bounds of reasonable probability that these play a most important part in the production of displacements of the large intestines. The cause of the disordered nervous action which leads to this may, from its physiological interest, be briefly dealt with. Apart from such obvious explanations as errors in feeding (see, in this connection, pp. 186, 187, 198, 199, 265), the most common cause of derangement of the muscular action of the digestive canal is *work*. It is this which accounts for the majority of colic cases occurring towards the end of the day, for the frequency with which the seizure occurs at or shortly after work, especially that of an exhausting nature, and for the practical absence of colic among non-working horses. We have even known a horse in a cavalry charge rupture the ileum as completely as if the parts had been torn asunder by hand; and this, it will be remembered, is the thickest and stoutest portion of the small intestine, and the least likely to suffer laceration. The connection between such a lesion and an exhausting gallop is at present not very apparent, but the fact is undoubted.

The whole subject is of profound practical interest, and more has been here said than is commonly considered to come within the province of physiology; but the basis of exact clinical knowledge is sound anatomy and physiology, and we feel that the physiological aspect of digestive disorders has not yet received adequate attention. It must be borne in mind that the whole length of the digestive tract is a chemical laboratory concerned in the analysis and synthesis of food-stuffs, isolating and retaining those which are of use, getting rid of those which are useless, and rendering harmless those substances capable of acting injuriously. Not only is it a laboratory where the above analytical operations are carried out, but it is also a factory where the chemical reagents necessary for this process are prepared beforehand. So thoroughly is the analysis performed, that the most complex bodies are broken down into the simplest products. Can it be wondered at that the chemical processes may sometimes fail, and disorder result ?

We see a faithful reflex of the laboratory processes in the disorders of the canal—the **diarrhœa** which is full of beneficence, **impaction** which indicates a loss of muscular power and physical alteration of the contents, acute **tympany** which announces active fermentation, **rupture** which indicates the strain on the walls of the apparatus; these, and other disorders too numerous to be dealt with, and which no mere mention can explain, give some idea of the penalty paid by horses for the doubtful privilege of domestication. The term 'digestion of a horse' has been framed in absolute ignorance of the real facts. There is no animal in which these organs are more readily disturbed, and none in which they are the subject of such acutely painful and mortal lesions. On the other hand, the ass appears to possess almost complete immunity, in spite of the coarseness of his forage. If, as stated above, work is a factor in the production of stomach and intestinal trouble, it may well be that the slow, steady pace of the ass is his salvation. The mule, however, is very liable to diseases of the digestive canal, though less so than the horse.

The ruminant, from the peculiarity of its physiological arrangement, is far more liable to stomach than to intestinal trouble; **tympany, impaction, paralysis,** and **inflammation** of one or more of the compartments are common. In spite of the size of the œsophagus, impaction is frequent—there is here a marked contrast to the horse, in which the tube is narrow and impaction uncommon—and **calculi,** the formation of which is a special feature in the intestine of the horse, are found in the stomach of the ox, though arising from very different causes. **Strangulation** of the bowels in the ox is not unknown, but limited to a special variety due to anatomical conditions.

Parasitic trouble is in all animals a prominent pathological feature, the digestive canal from the mouth to the anus being liable to infection with numerous varieties of parasites, forming also the main channel of parasitic entry for other parts of the body. Parasitic aneurism of the mesenteric artery has been regarded as a cause of colic in horses, though this does not accord with the writer's experience. A horse may have this vessel extensively diseased and have never suffered from colic. The ass is practically never free from parasitic invasion of the mesenteric arteries, yet he appears to possess immunity to colic.

CHAPTER VI

THE LIVER AND PANCREAS

SECTION I.

The Liver.

In considering the function of the liver it is necessary to bear in mind its peculiar blood-supply. Most glands of the body which are called upon to produce a secretion are for that reason furnished only with arterial blood, but the liver is an exception to this rule; the entire venous blood returning from the splanchnic area—viz., the bowels, stomach, spleen, pancreas, etc.—constitutes the material with which the liver is flooded. Blood derived from so peculiar and considerable an area must be of very mixed composition and charged with many products, some the result of secretory activity, others the soluble constituents of the elements of food, or, again, substances absorbed from the intestinal canal, which are by-products produced during the gradual breaking-down of the food substances. It is with this blood that the liver performs its various functions, and one of the most evident—viz., the secretion of bile—will be dealt with first.

Bile.

The bile is a fluid of an alkaline reaction, of bitter taste, of a specific gravity in the ox of 1·022 to 1·025, in the sheep from 1·025 to 1·031, and in the horse 1·005. The colour is yellowish-green or dark green in herbivora, reddish-brown in the pig, and golden-red in carnivora. These differences in colour depend upon the character of the pigment present. Bile taken from the gall-bladder is viscid, due to admixture with nucleo-albumin during its stay in the latter receptacle; that taken direct from the liver is relatively watery in consistence. The secretion contains no protein, which is somewhat remarkable; biliary pigments, bile acids, fats, soaps, lecithin, cholesterin, and inorganic salts are found in varying quantities. By the secretion standing in the gall-bladder the proportion of the solids is considerably increased, owing to an absorption of part of the water of the bile. The secretion in the horse contains no mucin, and, according to Ellenberger, there is very little mucin in the bile of sheep; what was believed to be mucin in ox bile, and what confers on the latter its ropy character, is now known to be nucleo-albumin.

The dried alcoholic extract of bile contains in the ox 3·58 per cent. of sulphur; in the sheep, 5·71 per cent.; and in the pig, 0·33 per cent. The gases found in bile are carbonic acid, and traces of oxygen and nitrogen. The chief inorganic salts are sodium chloride and phosphate, besides which are found salts of calcium, of magnesium, of potassium, of iron, with phosphoric and sulphuric acids; the sodium salts always exist in the largest proportion. The iron, which is found as phosphate, is probably derived from the hæmoglobin of the blood during the formation of the bile pigments.

The following table, showing the percentage composition of various biles, is compiled mainly from Ellenberger:

	Horse Bile.	Ox Bile.	Dog Bile.	Pig Bile.
Water	95	90·40	95·3	88·8
Solids	5	9·60	4·7	11·2
Bile acids Bile pigments Fat Mucin	—	8·30	4·1	10·1
Salts	—	1·30	0·6	1·1

Percentage Composition of the Ash of Ox Bile.

Sodium chloride	27·70	Manganese peroxide	0·12
Potassium	4·80	Phosphoric acid	10·45
Sodium	36·70	Sulphuric acid	6·39
Calcium carbonate	1·40	Carbonic acid	11·26
Magnesium	0·53	Silica	0·36
Iron oxide	0·23		

The differences found in the composition of bile probably depend upon whether it be taken from the gall-bladder or from a fistula, the former being the more concentrated.

The **Bile Pigments** are two in number—**bilirubin** and **biliverdin**; the latter is produced by oxidation from the former. Bilirubin is the colouring matter of human bile and of that of carnivora, whilst biliverdin is the pigment of the bile of herbivora. It is not uncommon to find both pigments in the same specimen of bile. Though the bile of the dog contains exclusively bilirubin as a pigment, yet the placenta of this animal is rich in biliverdin.

In the ox and sheep a pigment is present in bile which shows first a three-banded, and later, after standing, a four-banded spectrum. These bands are due to **cholohæmatin,** which is not a bile pigment proper. The pigments are insoluble in water, but soluble in alkalies; in the bile they are held in solution by the bile acids and alkalies. Bilirubin may be obtained from the gall-stones of the ox in the form of an orange-coloured powder, which can be made to crystallise in rhombic tablets and prisms. If an alkaline solution of bilirubin be exposed to the air, it becomes biliverdin by oxidation, and this latter pigment, by appropriate treatment, may be obtained as a green powder. Both colouring matters of the bile behave like acids, forming soluble compounds with metals of the potassium group, insoluble ones with those of the calcium group (Bunge).

On the addition of nitric acid (containing nitrous acid) to the bile pigments a play of colour is observed; this test is known as Gmelin's test. In the case of bilirubin the colours pass from yellowish-red to green, then to blue, violet, red, and yellow; each of these colours is indicativeo f a different degree of oxidation of the original bilirubin. Biliverdin gives the same play of colours, except that the initial yellowish-red is absent.

Although bilirubin has not been obtained from hæmoglobin, there is no doubt that this is the source of the pigment, for if hæmoglobin be liberated in the blood and enter the plasma, bile pigments appear in the urine; further, hæmoglobin may be readily decomposed, yielding a protein and hæmatin; and if this hæmatin be deprived of iron, the residue thus obtained is not very dissimilar in composition to bilirubin. We have previously mentioned (p. 15) that old blood-clots contain an iron-free substance known as hæmatoidin, and this is practically identical in composition with bilirubin. When red blood-cells disintegrate in the ordinary course of wear and tear, the liberated hæmoglobin is brought to the liver, and under the influence of the liver cells converted into the iron-free substance bilirubin or biliverdin. Part of the iron so liberated escapes from the body through the bile, but the greater part of it is retained, and again used in the formation of hæmoglobin by the organs which discharge this function.

Though biliverdin is the colouring matter of the bile of herbivora, yet the gall-stones found in the ox consist very largely of bilirubin combined with chalk; in the pig the same combination is observed. Bilirubin is said by Hammarsten to be constantly present in the serum from horse's blood, though not in that from blood of the ox, and Salkowski states that it is a normal constituent of the urine of the dog during the summer. In the large intestines both bilirubin and biliverdin undergo reduction, resulting in the formation of **stercobilin,** the colouring matter of the fæces in some animals. It is possible also that some of the pigment is reabsorbed from the intestinal canal, carried to the liver, and again eliminated. The value of this circulation of bile pigment is unknown.

The **Bile Acids** are two in number—**glycocholic** and **taurocholic acids;** they are formed in the liver by the union of **cholalic acid** with **glycine** or **taurine,** and exist in the bile as **salts,** in combination with soda. These salts are found in varying proportions in different animals; thus, glycocholate of soda is found in large quantities in herbivora, taurocholate principally in carnivora, while in the pig hyoglycocholic and hyotaurocholic acids are found. Both salts are soluble in water, have a markedly alkaline reaction, rotate the plane of polarised light to the right, and may be obtained in a crystalline form as highly deliquescent acicular needles. Glycocholic acid is diminished by an animal and increased by a vegetable diet. Taurocholic acid differs characteristically from glycocholic by containing sulphur, by which it shows its protein origin.

The **origin of the bile acids** is involved in obscurity. Cholalic acid is a non-nitrogenous body, whereas both glycine and taurine are nitrogenous. Glycine, also known as glycocoll, is a member of the important amino-acid group and a constituent of protein. Taurine, on the other hand, though an amino-acid, is not a constituent of protein; it can, however, be readily formed from cystine, which is a constituent of protein. It is assumed that glycine and taurine are derived from the disintegration of protein, but the precursors of cholalic acid are unknown. Glycine cannot be traced in a free state in the body, though, as we shall see later, it not only contributes to bile formation, but in the kidney, in combination with benzoic acid, produces hippuric acid. It is not known why glycine should predominate in some animals and taurine in others. It appears clear that the bile salts are formed in the liver cells. In the intestines a portion of the bile salts is reabsorbed, carried to the liver, and again excreted; or they may be split up in the intestines into their constituents, the glycine and taurine being carried to the liver to be re-utilised, while the cholalic acid is excreted. This economical measure, the second of its kind noted in dealing with the liver, has a twofold advantage, for not only can the glycine and taurine be used over and over again, but these bile acids are the best of cholagogues, and stimulate the production of bile. Pettenkofer's test for bile acids is performed as follows: A drop of the fluid is placed on a white earthenware surface, and to it is added a drop of a strong (10 to 20 per cent.) solution of cane sugar, and a similar quantity of strong sulphuric acid; a beautiful purple-red colour forms. The reaction is due to **furfurol**, which is produced by the action of the sulphuric acid on the sugar; the bile acids in the presence of furfurol give the purple colour.

Cholesterin finds its way to the liver for the purpose of being excreted. It is a substance found in many of the tissues of the body, but especially in the white matter of the nervous system. It is insoluble in water, but soluble in a solution of bile acids. When cholesterin finds its way into the bile, it is eliminated with the fæces. Cholesterin is found in very regular quantities in the body, and forms one of the principal constituents of certain gall-stones, and also, it may be added, of tumours in the lateral ventricle of the brain of the horse.

Lecithin is another waste product brought to the liver for excretion. It is of unknown physiological significance, but it has been suggested that it may serve to activate the lipase of the pancreatic secretion.

Secretion of Bile.—Bile is secreted under a very low pressure, which is the reverse of what occurs in the secretion of saliva; low as the pressure is—13 mm. (0·58 inch) of mercury—it is higher than that of the blood in the portal vein. If the pressure in the bile-duct be raised, the bile is reabsorbed, being taken up by the lymphatics of the liver, and so conveyed to the blood-stream. It is probable that the majority of cases of jaundice are due to obstructive causes, though exceptions to this rule occur. The secretion of bile is continuous, whether the animal be in full digestion or fasting; the flow is not intermittent, as in the case of the saliva. Though continuous, it is not uniform; it reaches its maximum in the dog between the second and fourth hours after a meal; this is followed by a fall, and again about the seventh hour by a rise. A similar quantity curve is given by the pancreatic secretion, which suggests how closely these two fluids are co-operative in digestion, while it can be shown that a specific substance, *secretin* (see p. 218), which stimulates the production of pancreatic juice, also hastens the secretion of bile. Acids injected into the duodenum increase the flow of bile, even after all nervous connections are severed. This is due to the acid chyme converting the *prosecretin* into secretin, and this, as above stated, has a specific action on the liver cells.

The secretion of bile is increased by any agent which destroys the red blood-cells. A solution of hæmoglobin injected into the blood therefore produces an increase. The administration of bile increases its production; this is due to the bile acids having a specific action on the liver cells, and acting as cholagogues.

In those animals possessing a gall-bladder this receptacle is filled with bile during abstinence, but if it be empty, it is filled even during digestion. The reflux of bile from the biliary duct to the gall-bladder is caused by a sphincter-like contraction of that part of the duct which penetrates the wall of the intestine; in this way the bile is driven back along the cystic duct to the gall-bladder. The bile as formed is propelled along the bile-ducts by a contraction of the muscular coat of the tubes, but doubtless both the forcing onward of the bile and the circulation through the liver are largely assisted by the respiratory movements, during which the liver is compressed between the abdominal viscera and the diaphragm.

By some it is considered that no bile enters the bowel while the stomach is empty, but that the passage of acid chyme along the duodenum causes a reflex contraction of the gall-bladder, and an injection of bile into the intestine.

The **amount of bile** secreted varies, but is greater in herbivora than in carnivora. Colin's experiments gave him the following amounts as hourly secretions:

Horse	-	250 to 310	grammes	(8 to 10 ounces) per hour.
Ox	-	93 to 120	,,	(3 to 4 ounces) per hour.
Sheep	-	8 to 150	,,	($\frac{1}{4}$ ounce to 5 ounces) per hour.
Pig	-	62 to 150	,,	(2 to 5 ounces) per hour.
Dog	-	8 to 16	,,	($\frac{1}{4}$ to $\frac{1}{2}$ ounce) per hour.

The **Use of the Bile** from a digestive point of view is disappointing, inasmuch as it does not digest in the same sense that pepsin and trypsin do. The bile and pancreatic fluid are intimately connected in function, for which reason the secretions are poured out into the bowel, either close together, or, as in some animals, by a duct practically common to the two glands. As the horse possesses no gall-bladder, the secretion is poured into the intestine as fast as it is prepared; not so in the ox, sheep, pig, and dog, where most of it is stored up in a capacious receptacle until required. The explanation offered for the horse having no gall-bladder is that as digestion, under ordinary circumstances, never ceases, the bile is poured into the bowel as fast as it is secreted, but that in the case of other animals it is poured out only when the contents of the stomach are passing out into the intestine. This explanation, however, does not meet all the difficulties of the case. The following animals, like the horse, have no gall-bladder: the camel, elephant, rhinoceros, tapir, and deer.

The bile being alkaline, its first action on the chyme is to neutralise the gastric juice, and to precipitate the albumoses and peptones. One effect of this is probably to delay the progress of the chyme along the bowel, by which means absorption is assisted.

Bile has a solvent and emulsifying effect on fats, being in this respect more active in the presence than in the absence of pancreatic juice. Bile cannot split up fats into fatty acids and glycerol, but its presence increases threefold this action of the pancreatic fluid. Once the fats are split, the bile takes an active share in digestion, for fatty acids, which are insoluble in water, are soluble in bile salts and lecithin, the latter greatly increasing the power of the bile salts as fat solvents. The fatty acids form soaps with the alkali of the intestinal and pancreatic secretions, and these are also dissolved by the bile acids. The solution of soaps so formed makes the emulsifying effect of the bile permanent and the absorption of fat easier. In Voit's experiments on dogs it was found that by cutting off the flow of bile to the intestine the absorption of fat fell from 99 per cent. to 40 per cent.; the solvent action of bile on fat is the chief digestive function of this fluid, but in its action on fat it works in conjunction with the pancreatic secretion. We shall see later (p. 265) how the presence of bile increases the energy of the pancreatic fluid in the emulsification of fat. Bile has no action on proteins. According to Hofmeister, the bile of the ox, sheep, and horse converts starch into sugar, while the bile of the pig and dog possesses no such power, or only to a limited extent. It has been said that bile has an antiseptic influence on the intestinal contents, protecting them from putrefaction, for it has been found that when it is prevented from entering the bowels, constipation and extreme fœtor of the intestinal contents result. Bile, however, is not a true antiseptic. The clay-coloured fæces obtained in jaundice are probably due to the presence of unacted-on fat; the fat encloses the proteins which putrefy, hence the odour. The bile acts as a natural purgative, and keeps up intestinal peristalsis; by so doing it hurries the food residues out of the system before they undergo excessive putrefactive decomposition.

Glycogen.

It is quite certain that the largest gland in the body must have some other function than that of the secretion of a fluid of comparatively unimportant digestive power,. and such is the case; the liver manufactures and stores up in its cells a peculiar substance known as glycogen or animal starch. Glycogen is spoken of as a starch, though it differs from vegetable starch in many important characteristics; thus, it is soluble instead of insoluble in cold water, and it is stained reddish-brown instead of blue by iodine. Though glycogen may be detected in the liver substance by the iodine test, it is now believed that it is not actually deposited in the cells, but held there in weak chemical combination; for it cannot readily be extracted from the liver by means of cold water, whereas outside the body it is readily soluble in water.

The literature of the formation and use of glycogen is extensive, perhaps no substance has given rise to greater controversy; yet the glycogen theory which is accepted to-day is the one originally proposed by Claude Bernard, who was the discoverer of this singular substance.

The sugar in the food, together with that derived from starch-conversion, finds its way by means of the intestinal vessels into the portal vein, which may contain 0·4 per cent. after a heavy carbohydrate meal or 0·2 per cent. during starvation; from here it passes into the liver, where, under ordinary circumstances, it is stored up as glycogen, being, in fact, reconverted into a kind of starch, and when required gradually doled out by the hepatic veins to the system as sugar. The liver regulates the amount of sugar which should pass into the blood; so much, and no more is admitted to the circulating fluid, the amount varying between 0·05 and 0·15 per cent. The sugar in the blood in the ox was estimated by C. Bernard at 0·17 per cent., in the calf at 0·1 per cent., and in the horse at 0·09 per cent. There is consequently a great difference between the sugar content of the portal and that of the hepatic vein. When the liver fails to regulate the amount of sugar in the blood diabetes is produced, and this occurs when the amount of sugar rises to more than 0·2 per cent. It is doubtful, however, whether this is a common form of diabetes.

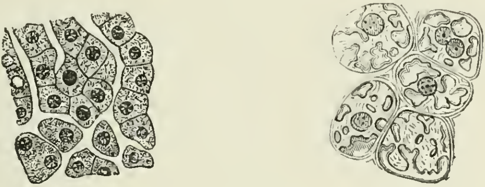
FASTING. AFTER FOOD.

FIG. 82.—LIVER CELLS FROM THE DOG DURING FASTING AND AFTER FOOD (WALLER, AFTER HEIDENHAIN).

During fasting the cells contain no glycogen; after receiving food they become swollen with this substance.

The glycogen which is stored up in the liver for future use may in two or more days be made to disappear by starving and *working* the animal, the material in this way escaping from the liver as sugar, and passing into the general circulation through the hepatic veins. The administration of arsenic or of phosphorus, by the action of these substances on the liver cells, also causes a marked diminution in the amount of glycogen, while strychnine in poisonous doses is most effective in this respect, owing to the excessive muscular contractions produced.

The storing up of glycogen by the liver and its subsequent utilisation are very closely allied to a similar process in the vegetable kingdom; the starch in the leaves of plants may pass down the stem as sugar for the purpose of nourishment, and be again formed into starch. Similarly in the animal the starch must be first converted into sugar before the bloodvessels of the bowel can take it up, then in the liver once more converted into a starch substance, glycogen, and lastly, again into sugar before being finally used by the tissues. The sugar formed from starch in the bowel is maltose, while that formed in the liver from glycogen is dextrose. This conversion of glycogen into dextrose is due to the presence of a ferment in the liver cells.

The total amount of glycogen obtained from a given quantity of food is not wholly stored in the liver; the latter organ can only hold a limited amount, which, on a rich carbohydrate diet, does not exceed 17 per cent. in the dog, and in the rabbit 27 per cent., of its weight, and in other animals is less. We know, as a fact, that the liver, having taken up all the sugar it can from the portal vessels and converted it into stored-up glycogen, allows the balance to pass through the hepatic veins into the general circulation as sugar, and that this balance is deposited in other organs, principally the muscles, as glycogen for future use. The muscles of well-fed animals contain in this way a considerable quantity of glycogen; even after nine days' starvation in the horse from 1 to 2·4 per cent. has been found in them. It may be stated that the muscles hold ordinarily as much glycogen as the liver, but it takes longer, by means of work and starvation, to free the muscles from glycogen than to clear the liver. The presence of glycogen in muscle is not essential to contraction, for there are muscles in which no glycogen is found, and in which, nevertheless, active contraction takes place. In the muscles of the embryo, before striation has occurred, the amount of glycogen is something considerable; as much as 40 per cent. of the dry material of the embryo muscle may consist of this substance. As striation appears the glycogen leaves the muscles to a great extent, and the liver takes on the process of production.

The Use of Glycogen.—The muscles and liver are not the only seats of glycogen deposits; traces may be found practically everywhere in the body, but none can be found in the blood-plasma. The existence of glycogen in the embryonic muscle points to its use in active nutrition and rapid growth; further, it is found in the placenta, where it is used for the nourishment of the fœtus. In the adult the chief use of glycogen is to facilitate the metabolic production of muscular energy and animal heat, and this is effected by the oxidation of dextrose to carbon dioxide and water. This oxidation does not occur in the blood; the destruction of sugar (*glycolysis*) occurs in all active tissues, especially in muscles and glands. It can be shown that there is less sugar in the veins of an active muscle than in the arterial blood supplying it. It was found experimentally that the muscles of the upper lip of the horse used up in a state of activity 3·5 times more dextrose than during rest, and the actively secreting parotid gland of the same animal used more sugar than the resting gland.

The **sources of glycogen** have been a fertile subject of discussion and an object of experimental inquiry. It was natural to consider, as we have so far done, carbohydrate material as the chief contributing agent; it was less certain that protein contributed, while the consensus of opinion was against fat taking any share in the process. We must examine each of these points in more detail.

We have learnt that starch is not absorbed as starch, but, depending upon the nature of the diastatic ferment, is converted into maltose, or maltose and some dextrin, and subsequently into dextrose. These sugars are readily converted into glycogen by the liver cells by the process of dehydration. Cane sugar and milk sugar are not readily converted into glycogen, but since these double sugars undergo inversion in the intestinal canal before absorption—cane sugar into dextrose and levulose, and milk sugar into dextrose and galactose—they may in these forms be readily converted into glycogen. All carbohydrates, then, which are capable of being changed into dextrose or levulose, may be converted into glycogen, provided they pass through the laboratory of the intestinal canal. For example, cane sugar, if injected subcutaneously, passes unchanged into the urine; in order to be converted into glycogen it must pass through the intestine.

The effect of protein on glycogen formation is not so easily explained. It is observed that in diabetes, though all carbohydrate food be withheld yet sugar may appear in the urine on an exclusively protein diet; the same thing is observed in the experimental glycosuria which may be produced by the administration of a substance known as ‘phloridzin,’* and, furthermore, sugar may be produced even when the animal is starved. The conclusion appears irresistible that protein can produce sugar, and this is explained by saying that certain proteins split into a nitrogenous and a non-nitrogenous portion, the former being converted into urea, while the non-nitrogenous residue is converted into sugar, and may thus give rise to glycogen. It is now known, however, that proteins which do not contain a carbohydrate group, such as casein, may take a share in the production of glycogen; this strengthens the belief that protein may give rise to sugar. But the carbohydrate portion of the protein molecule which yields glycogen is not the only protein source of sugar; it is now known that sugar can be formed from some of the end-products of the pancreatic digestion of proteins (p. 263)—viz., the amino-bodies, of which *glycine* and *alanine* may be completely converted into dextrose, and *glutamic* and *aspartic* acids partly so converted.

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* Obtained from the roots of the apple-tree.

There are a few observers who regard fat as a source of glycogen, and there is some evidence to show that it may contribute, for it has been said that glycerin acts as a sugar former. If this is so, the conversion of fat into glycogen, through its splitting up in the intestinal canal into fatty acid and glycerin, would not be a difficult matter. On the other hand, experiment shows that when an animal is fed solely on fat, the glycogen disappears from the liver as quickly as it does in starvation. Nevertheless, it is an interesting fact that during prolonged starvation, even forty to ninety days, the amount of sugar in the blood is practically constant, and its only sources at this time are the protein and fat of the body. The question is, therefore, very far from being settled.

The Liver Ferment.—When the liver is rapidly excised from the body of a recently killed animal which has been appropriately fed, it contains a quantity of glycogen; if it is allowed to stand, the glycogen gradually becomes reduced in amount, and sugar takes its place; finally, all the glycogen disappears. This change is brought about by a diastatic ferment in the liver cells which changes the glycogen into sugar. If the liver on removal from the body be rapidly minced and boiled, the ferment is destroyed, and dextrose is not formed.

How the Supply of Sugar is Regulated.—We have seen that in the tissues the glycogen in the form of dextrose is oxidised into carbon dioxide and water, producing heat and energy. After every meal a store of glycogen accumulates in the liver for subsequent use, and in spite of changes in the amount of diet, differences in the amount of daily work performed, or of heat produced, yet the sugar in the hepatic veins maintains a perfectly regular proportion of from 0·1 to 0·2 per cent. The means which control the issue of sugar from the liver are very imperfectly known; they are probably under the influence both of the nervous system and of an *internal secretion* produced by the pancreas, and the subject will be again considered when the pancreas is dealt with. One thing seems clear—that the liver itself is unable to regulate the amount, and that whenever either the nervous or the chemical factors fail, it allows sugar to pass into the blood in a proportion largely over and above that which can be oxidised (*hyperglycæmia*), with the result that since the kidney is permeable to dextrose present in blood to a greater extent than 0·2 per cent., sugar escapes with the urine (*glycosuria*), constituting the disease known as **diabetes.** The sugar excreted with the urine is, of course, lost to the system, and constitutes a heavy drain on the body, which in consequence rapidly wastes. This condition may also be experimentally produced in the dog by removal of the pancreas.

We have studied two uses of the liver—viz., the formation of bile and the storing up of glycogen—but there are other functions of this gland to consider.

The Formation of Urea.—When the complex protein molecule of the food is broken down into simpler end-products, one of these, known as 'urea,' is excreted by means of the kidneys; this substance, however, is not formed in these organs It is proved conclusively that part, at least, of the urea in the body is formed in the liver. During the process of protein disintegration certain amino-acids, known as *leucine* and *tyrosine*, are produced, either in the intestinal canal under the influence of pancreatic digestion, or in the living cell as the result of the breaking down of protein. Under any circumstances the leucine undergoes a series of oxidative changes mainly in the liver, which result in the formation of urea. The further facts regarding the formation of urea are best dealt with in the section devoted to the kidneys.

As the result of protein decomposition in the intestinal canal certain aromatic compounds are formed; these are united with sulphuric acid, and got rid of by the kidneys as conjugated sulphuric acids. In this combination the originally *poisonous protein products* are converted into non-poisonous ones, and this change is effected in the liver (Bunge). In this we have a very important function of the liver demonstrated—viz., as a neutraliser of poisons introduced into the blood by the intestines. It is a noteworthy fact that many metallic poisons are also arrested in the liver—for example, mercury and arsenic.

Summary.

The numerous and complicated changes produced by the liver may thus be summarised: It forms bile, regulates the supply of sugar to the system, and stores up as glycogen what is not required. It guards the systemic circulation against the introduction of certain nitrogenous poisons, such as ammonia, by transforming them into urea, and against other poisons of protein origin by converting them into harmless products, by conjugation with alkaline sulphates.

In animals, other than herbivora, the liver acts as an important fat depot, obtaining its store of fat from adipose tissue. The transport probably takes place in the form of fatty acids and glycerol, the former being first desaturated and then broken down into lower fatty acids. This transport of fatty acid to the liver from other fat storehouses in the body takes place to a great extent in various diseases, and after the action of certain poisons such as phosphorus.

Section 2.

The Pancreas.

The fluid secreted by the pancreas performs certain important functions in digestion. It has been remarked that there is scarcely any animal which does not possess a secretion allied to the pancreatic; even those invertebrates without a peptic or a biliary apparatus are in possession of a pancreatic one. From the resemblance of the pancreas to the salivary glands, it has been termed the 'abdominal salivary gland.'

The pancreatic fluid from herbivora can be obtained only with extreme difficulty; to establish a pancreatic fistula in the horse is a formidable operation, necessitating an incision from the sternum to the pubis and the turning back of the bowels. Colin established such fistulæ both in the horse and in the ox, but the profound impression on the nervous system produced by such extensive interference must considerably affect the character of the secretion and the amount manufactured.

Pancreatic fluid is an alkaline fluid, clear, colourless, like water, and though viscid in some animals, is not so in the horse or ox. It has a saltish, unpleasant taste, and a specific gravity of about 1·010; the viscid secretion of the dog has a specific gravity of 1·030. The following analysis of the fluid in the horse is given by Hoppe-Seyler:

Water	98·25			
Solids	1·74	Organic matter	0·88,	containing 0·86 of ferments.
		Salts	0·86,	containing much sodium phosphate.

Schmidt found the fluid of the dog to have the following composition:

Water	90·00			
Solids	9·92	Organic matter	9·04,	
		Salts	0·88,	containing much sodium chloride.

The salts present are sodium chloride in abundance, potassium chloride in traces, sodium carbonate and sodium phosphate, calcium and magnesium phosphates in small quantities. To the sodium carbonate is due the strong alkaline reaction. The organic solids are remarkable for the amount of protein present in them; they vary in amount with different animals—for example, 9 per cent. in the dog, and 0·9 per cent. in the horse. The pancreatic secretion is remarkable for containing, in addition to the substances already named, three enzymes, which act on different food substances.

Mechanism of Pancreatic Secretion.—The pancreatic secretion is influenced by special secretory nerves; stimulation of the vagus or splanchnic may, after a long latent period, give rise to a secretion, though it is not yet settled that these fibres produce secretion during the act of digestion. The outpouring of the acid chyme from the stomach into the duodenum at once causes a secretion of pancreatic juice, and at one time it was supposed the acid acted on the secretory nerves and produced a secretion reflexly, for this action could be reproduced experimentally. Bayliss and Starling, however, demonstrated the remarkable fact that if an extract of the mucous membrane of the duodenum, or of the jejunum, be made by scraping the bowel, and by then acting on the scraping by weak hydrochloric acid, a substance may be obtained which, when injected into the blood, produces a profuse pancreatic secretion. To this internal secretion of the intestinal cells they gave the name **Secretin,** the nature of which has not been determined. Two facts are, however, clearly established—first, that it is not a ferment, as it is not destroyed by boiling; and, secondly, that the action of acid is an essential part of the process, for if the mucous membrane of the bowel be extracted with either water or saline solution, secretin is not obtained. It is the *acid* chyme, therefore, which, acting on the mucous membrane of the intestine, produces secretin; this is absorbed by the blood, and thus produces its specific action on the pancreas. Within a minute or two of our introducing a 0·4 per cent. hydrochloric acid into the duodenum pancreatic juice flows into the intestine. The acid produces the same effect if introduced into the jejunum, but not if into the ileum.

Secretin is not a protein; it is not destroyed, as stated above, by boiling, and it is soluble in alcohol and in ether. Prosecretin exists in the intestinal mucous membrane; it may be extracted with physiological salt solution, and though unable itself to promote pancreatic secretion, it may be converted into an active secretin by the action of acid or by boiling. Secretin from one animal will increase the pancreatic flow in another, either of the same or of a different species. Secretin is a *hormone* or chemical messenger.

As a secretion can be obtained from the pancreas either by stimulation of certain nerves or by introducing into the blood a specific chemical substance, it would appear that under normal conditions both processes may be operating in its production, and that there may be, as in the case of the gastric juice, two parts in the secretion. Evidence has been brought forward to show that the secretions obtained by these two stimuli differ considerably. The nervous secretion is thick, rich in ferments, poor in alkali, and the trypsin it contains is active. The effect of atropine is to suspend secretion, while that of pilocarpine is to stimulate it. The chemically produced fluid is thin and watery, contains but a small amount of ferment, and an abundance of alkali. The secretion is unaffected by atropine, and its trypsin is not in an active form when secreted.

Uses of the Secretion.—The pancreatic juice is poured into the bowel in the horse and in the sheep by an opening common to the pancreas and liver, while in the ox, pig, and dog, the ducts of the liver and pancreas are separate, but open into the bowel within a short distance of each other.

This juice is essentially a digestive fluid, and acts on the three classes of food-stuffs—viz., proteins, fats, and carbohydrates. To enable it to effect this, it contains three ferments or their precursors—viz.:

A Proteolytic Enzyme which acts on proteins (*Trypsin*).
A Diastatic Enzyme which acts on carbohydrates (*Amylopsin*).
A Lipolytic Enzyme which acts on fats (*Lipase or Steapsin*).

Earlier observations appeared to show that the proportion of each of these ferments in the secretion depended on the character of the food; if, for example, the food was rich in fat, the secretion would be rich in lipase. It was also held that the nature of the food determined the predominance of each enzyme, as well as the amount of fluid to be secreted. The specific action of food-stuffs on the production of pancreatic enzymes is no longer regarded as constant or characteristic. As a rule secretion reached its maximum in the dog between the second and fourth hour after taking food, corresponding to the greatest activity of the liver. In dogs which have been starved active secretion of bile, pancreatic juice, and intestinal fluid, associated with gastro-intestinal movements (see p. 233), take place, it is said, every two hours, and last for twenty minutes. The cause of this is by no means clear. All the fluid thus poured out is reabsorbed.

Trypsin.—Pancreatic juice taken direct from a fistula in the duct has little or no action on the proteins of food, but if the same fluid be allowed to become contaminated by the intestinal contents it at once becomes active. Evidently the addition of a something from the bowel has brought about a marked change in the proteolytic character of the secretion. Investigation shows that though the secretion taken direct from the pancreas contains the precursor of trypsin—viz., **trypsinogen**—yet in this form the ferment is unable to act on the protein of food until it has itself been acted upon by another ferment. This ferment is derived from the mucous membrane of the intestinal canal. A ferment acting on a ferment has been described as a **kinase** or activating ferment, and as this one is derived from the bowel it is called **enterokinase,** a very small amount of which is capable of converting inactive trypsinogen into active trypsin. It is remarkable that of the three ferments secreted by the pancreas, trypsin is the only one which is secreted in an inactive condition. Pavlov considers this to be due to the fact that if trypsin were active *in* the pancreatic juice, it would destroy its fellow-ferments, but that in the bowel these ferments are protected.

The fact that extracts of pancreas, as usually obtained from a slaughter-house, may be made more tryptically active by the addition of a little dilute acetic acid, does not, according to the modern theory, imply that the acid has converted the trypsinogen into trypsin, as has usually been supposed. The pancreas used in the preparation of these extracts is already contaminated with minute quantities of enterokinase, the activity of which is greatly increased by neutralising the alkalinity of the extracts. If a pancreas be obtained under conditions which insure the absence of any admixture with even traces of enterokinase, extracts of such a pancreas cannot be rendered more tryptically active by the addition of dilute acid (Starling). It is now believed that the conversion of inactive to active trypsin may be effected by salts of calcium and of magnesium, as well as by enterokinase.

The action of trypsin on proteins is most interesting. The protein molecule is very complex; the use of trypsin is to split it up into simpler products, with the object of facilitating its absorption. As we shall point out later, no food substance is taken up excepting in its simpler form, and the proteins of oats, barley, hay, or flesh, have to be reconstructed in order to form part of the tissues of the living animal. Trypsin acts on the large protein molecule, and breaks it down, producing a number of simpler bodies of smaller molecular weight; on these the tissue-cells set to work, and by a process of synthesis construct the form of protein needed by the body. It can be easily shown that the action of trypsin on protein is much more satisfactory and thorough if the protein has previously been acted upon by pepsin. Trypsin, like pepsin, produces albumoses and peptones; but the process does not stop at peptone; no peptone can be found in the blood, and none remains after a prolonged pancreatic digestion. The effect of the action of trypsin on proteins is nearly as complete as that of boiling protein with acid. In each case the hydrolysis results in the production of a large number of simpler end-products, chiefly of amino-bodies. Yet it would appear clear that the products obtained by acid hydrolysis are not quite the same as those produced by tryptic hydrolysis, for dogs may be kept in health when fed on the split products of pancreatic digestion, with a sufficiency of carbohydrates and fat, while the split products of acid hydrolysis cannot be so utilised. This question will be considered again in dealing with nutrition, but the subject is of interest here as showing that the laboratory of the body reduces the complex protein molecule into many simpler substances, which can be reproduced outside the body by active chemical means, and yet are not quite the same, for the material artificially produced by means of boiling acid is of no subsequent use to the body, whereas that produced in the system can be utilised.

The amino-bodies resulting from tryptic digestion are mainly organic acids containing either one amino (NH_2) group, or two such groups in union with carbon. Among the mon-amino-bodies are leucine, tyrosine, glycine, aspartic acid, glutamic acid, and tryptophan. Of the diamino-bodies, lysine, arginine, and histidine are present.

It should be stated that another view regarding the breaking down of protein into simpler substances exists—viz., that the whole protein molecule is not split up by tryptic digestion, but that a nucleus remains which in chemical character comes between a peptone and amino-bodies. It is described as a *peptid,* or more generally as a *polypeptid*, as these bodies consist of amino-acids which are linked together with the loss of one molecule of water for each pair. The polypeptid may by acid hydrolysis be converted into amino-bodies. It is suggested that the polypeptid serves as a starting-point for synthesis, for the protein substances taken in as food have to become converted into the tissues of the living animal, reconstructed in part from the amino-bodies, and the necessary synthesis, it is suggested, occurs around, or is directed by, the polypeptids. Whether or not this is correct does not in any way affect the important statement that all protein received as food is foreign to the body, and that before it can be built into the tissues of the living animal it has first to be pulled to pieces, and then again constructed.

Should any protein or peptone have escaped the action of pepsin and trypsin, it may be attacked by another enzyme found in the intestinal mucous membrane, known as **erepsin,** which also has the power of breaking down albumoses and peptones into leucine and tyrosine. Erepsin is found in most of the tissues of the body, and so is not specific to the intestine.

Under the influence of bacterial action numerous decomposition products may be split off from protein; among others, aromatic bodies are formed—phenol, indol, and skatol, the latter accounting for the fæcal odour of a pancreatic digestion mixture. These substances are produced from tryptophan, one of the end-products of the primary decomposition of proteins.

It is here desirable to draw attention to the fact that *secretin, enterokinase,* and *erepsin* are all derived from the mucous membrane of the intestinal canal. Care must be taken to avoid confusing them. The second and last are ferments, secretin is not. The function of secretin is to cause the production of pancreatic juice, that of enterokinase is to endow one of the ferments of the pancreatic juice with its remarkable proteolytic properties, while erepsin breaks down albumose and peptones into amino-bodies.

Amylopsin, the diastatic ferment, has an action on starchy food similar to that of ptyalin, but more rapid and more active, for it can deal with raw starch; the final products are maltose and achroodextrin. The hydrolytic action of amylopsin stops at maltose and achroodextrin, but these are in turn attacked by the **maltase** of the succus entericus, and converted into dextrose before absorption. All starchy food which has escaped conversion in the mouth and stomach is also acted upon in the intestines by maltase.

Lipase or **Steapsin** is the fat-splitting ferment of the pancreas; it possesses the remarkable power of breaking up fats into fatty acids and glycerol, and does this with the object of promoting their absorption. We have learned a little of this action in connection with the bile (p. 252), but must look at the matter now in somewhat greater detail. The power of fats to form emulsions is of great value in digestion. In the condition of emulsion the fat is very finely divided; milk is a secretion in which the fat is typically emulsified. Emulsion can also be brought about by mixing fat with gum, egg-white, and soap solution. The only fat emulsion received by animals as food is when they are young, and it is said that the wall of the stomach in young animals contains a gastric lipase which deals with this. If so, this section of the alimentary canal is of great importance in those animals where the pancreas is functionless in early life, a natural condition in man; in herbivora the pancreas is probably in active work at a month old. The fat-splitting power of pancreatic lipase is very marked, but, as mentioned at p. 252, is greatly increased by admixture with bile. When fats are split the fatty acids unite with the alkali of the intestinal and pancreatic secretion, and form soaps. We have seen the action of the combined bile and lecithin in dissolving fatty acids and soaps, and the physiological importance of this, for until solution is effected absorption is impossible. Without the assistance of bile no solution of fatty acids and soaps would occur as the result of the action of lipase. The removal of the soaps by absorption permits the lipase to continue its action.

As free fatty acids, soaps, and glycerol, the fat enters the villus and gains the chyle vessel. At one time it was believed fat in fine emulsion passed between the epithelial cells of the villus, but this is now held to be wrong. The oil globules seen in the villus represent the newly reconstructed fat, for the soluble products of fatty acids, soaps, and glycerol have no sooner got into the villus than neutral fat is reconstructed. Some think this is brought about by the *reversible action* of lipase, others believe the effect is due to the living cells of the villus, and is not the result of the action of a ferment. The fat so formed enters the lacteals, passing by the thoracic duct finally into the blood. Oil globules in the blood could not pass along the capillaries, and plugging of the vessels would occur. This is prevented by a change brought about in the blood, by which the fat is rendered soluble, dialysable, and capable of passing through the capillary wall. The method by which the blood effects this change is unknown; it is said, however, that lipase may be found in the blood, muscles, liver, and other glands, and, if so, this will account for fat embolism not occurring in the vessels, and also explain why the tissues are able to draw on their body fat as required, for this must be brought into solution before it can pass back into the blood.

Lipase is readily destroyed, so that, unless quite fresh, it does not do its work in artificial digestions. It is believed that a portion of the lipase is secreted in the inactive condition as a zymogen, or pro-enzyme form, and that this is activated by the action of the bile acids and lecithin. Whether this is so or not, the dependence of the pancreatic secretion on the co-operation of the bile is highly important.

On pp. 194, 197 we have alluded to Pavlov's work on the quantity and quality of the gastric juice being regulated by a specific action on the part of the food itself. The same observer held that the ferment contents of the pancreatic juice were adapted to the character of the food; for example, the lipase is increased by a fat diet. A definite and unchanging diet leads to the formation of a pancreatic juice, which is unable to deal effectively with a sudden change in food. If this were proved to be true, its practical bearing on the feeding of animals would be far-reaching. As a profession we have recognised for years the disastrous effects of sudden changes in diet; modern science offers a possible explanation of these effects. The whole matter is probably regulated by an internal secretion.

The **Changes occurring in the Cells** of the pancreas correspond very closely to those described for the salivary secretion.

When a pancreas or lobe of a pancreas has been at rest for some time the cells forming it are rendered very indistinct; the lumen of the alveolus is nearly obliterated by their swollen condition, and the cells are seen crowded with granules; these are so arranged that the margin of the cells presents a clear or fairly clear zone, while within this there is an intensely granular zone (Fig. 83, A). The minute granules filling the cell are the mother-substances of the secretion. When activity commences the granules appear to pass centrally towards the alveolus, leaving the cells comparatively clear excepting those portions immediately abutting on the alveolus, which even in the exhausted condition remain granular. These changes result in the cells becoming distinct and clearly defined, and, moreover, as they have emptied their granular contents into the alveolus as pancreatic secretion, they have consequently become much smaller. The narrow clear zone seen in the resting gland has now become broad, the previously choked alveolus is clearly defined, whilst the nucleus of the cell, which was hidden in the charged condition, can easily be seen in the exhausted gland (Fig. 83, B). These changes were worked out by observations on the pancreas of the living rabbit by Kühne and Sheridan Lea.

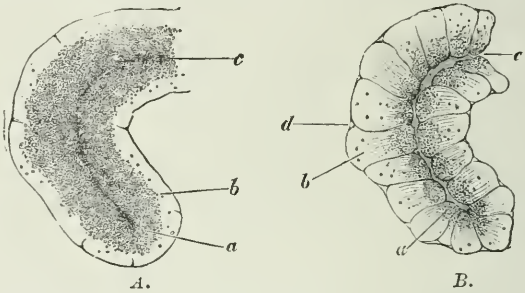

FIG. 83.—A PORTION OF THE PANCREAS OF THE RABBIT (KÜHNE AND SHERIDAN LEA). A, AT REST; B, IN A STATE OF ACTIVITY (FOSTER).

a, The inner granular zone in A is larger and more closely studded with fine granules than in B, in which the granules are fewer and coarser. *b*, The outer transparent zone is small in A, larger in B, and in the latter marked with faint striæ. *c*, The lumen is very obvious in B, but indistinct in A. *d*, An indentation of the junctions of the cells seen in the active but not in the resting glands.

Amount of Secretion.—From the investigations of Colin and others we know that in most animals the secretion of pancreatic juice is continuous, though not uniform. In ruminants the largest secretion is towards the end of rumination; in the dog the maximum is reached between the second and fourth hours after feeding, this maximum being followed by a fall, and about the seventh hour by a rise. It will be remembered that the secretion of the bile gives a similar curve. In the dog it is generally considered there is no secretion during starvation, but that immediately food begins to pass out of the stomach the pancreas becomes active. In this connection, however, it is desirable to remember that, according to some observers, a starved dog will actively secrete pancreatic juice for twenty minutes every two hours. The continuous secretion of the gland in herbivora is provided for by the lobes not all being active at the same time. In the ox the amount of juice secreted is about 265 grammes (9 ounces) per hour, in the horse it is much the same, in the sheep 7 to 8 grammes (about $\frac{1}{4}$ ounce), in the pig about 5 to 15 grammes ($\frac{1}{6}$ to $\frac{1}{2}$ ounce) per hour, and in the dog still less, 2 to 3 grammes. There is no necessary ratio between the size of the animal, the weight of the gland, and the amount of pancreatic fluid secreted; carnivora secrete relatively more than herbivora.

The pressure under which the pancreatic juice is secreted is low; it is said to be equal to 18 mm. (0·67 inch) of mercury, which is very little greater than that of the bile.

Pancreatic Diabetes.*—If the pancreas of a dog be completely removed, there is a disappearance of all glycogen from the tissues, sugar appears in the urine within twenty-four hours, and the animal dies in the course of a month or less from diabetes, since the power of oxidising dextrose is lost. The dextrose consequently accumulates in the blood, and is separated by the kidneys. In addition to there being sugar in the urine, there is also an increase in the amount of fluid produced and an excess of urea; consequently there is intense thirst, and this is associated with a large appetite, in spite of which the animal wastes. If the depancreated animal be placed on a purely protein diet, no difference occurs in the amount of sugar excreted; even if no food be given sugar is still formed. If the removal of the gland is incomplete, glycosuria may still occur, but its effects will vary in intensity from fatal to transient, depending upon the amount of pancreas left behind; in fact, it is possible from experience to leave behind just sufficient (one-fourth to one-fifth) of the gland to prevent diabetes arising. In any case, fatal results may be avoided by grafting portions of pancreas beneath the skin, the presence of these preventing diabetes. This proves that the prevention of glycosuria does not depend on the pancreatic juice.

Regulation of the Sugar Supply.—Throughout these remarks on the glycogen question, we have assumed that the view originally put forward by Bernard is correct—namely, that the sugar resulting from the conversion of carbohydrates in the digestive canal is stored in the liver and muscles as glycogen, while a definite proportion of sugar remains in circulation. The chief opponent of this theory was Pavy, who believed that glycogen is never converted back into sugar, but is built up into fat and protein. Further, he denied the existence during life of a liver ferment capable of converting glycogen into glucose. He showed that egg-albumin was capable of being so treated, that it yielded a reducing sugar which was obtained from the carbohydrate group of the protein molecule, and that serum globulin behaves similarly; mucin and nucleo-albumin are also now known to contain the same substance. The importance of this discovery was considerable, as the production of sugar from protein, though suspected, had not been proved. The diet of the omnivora and herbivora contains more carbohydrate than can be accounted for in the muscles and liver as glycogen, and it is certain that all over and above that required for the production of sugar must be converted into fat, and some of it incorporated with the protein tissues. Nevertheless the Bernard doctrine explains why the percentage of sugar in the circulating blood is constant—viz., by the gradual doling out of glycogen as sugar from the liver under the influence of a ferment in that gland, and physiologists have, with but few exceptions, accepted his teachings.

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* This matter should be read in conjunction with the remarks on Glycogen, p. 252.

What we have now to consider is the manner in which this regulation is effected, in order that the sugar content of the blood, 0·2 per cent., may remain at a normal level. The first to throw some light on the process was Bernard, who showed that if the floor of the fourth ventricle be punctured temporary diabetes results, sugar appearing in the urine, while the liver uses up its glycogen. This spot in the medulla is known as the diabetic centre, and the puncture acts, not by destroying, but by stimulating its activity. This is proved by the fact that if the animal be starved before the puncture is made no sugar appears in the urine, as no glycogen exists in the liver. The nerves passing to this centre—the afferent nerves—are contained in most of the sensory nerves of the body; if these are stimulated they act reflexly on the diabetic centre, and sugar in the urine results. The same occurs on stimulating the cerebral end of the divided vagus. The impulses from the diabetic centre to the liver pass down the spinal cord, and emerge in the anterior thoracic region with the inferior roots of the spinal nerves, and are connected with the inferior cervical and thoracic ganglia by the *rami communicantes ;* from these ganglia the impulses pass by means of the splanchnic nerve to the liver. Whether the splanchnic contains fibres which excite the secretion is unknown, but stimulation of the inferior cervical and thoracic ganglia produces glycosuria provided the splanchnic remains uncut. At one time it was considered that these results were due to vasomotor effect, and that vascular dilatation, rather than secretory activity, was brought about by stimulating the splanchnic, but it is now known that glycosuria is produced when the central end of the depressor nerve is stimulated, and the effect of stimulating this nerve is to cause a fall in abdominal blood-pressure. The impulses passing to the diabetic centre may, it has been suggested, originate in the contracting skeletal muscles by the compression of the muscle spindles. The heart muscle contains more glycogen than skeletal muscle; when the amount of glycogen in the latter has fallen to one-tenth or even one-thirtieth of the normal the heart muscle still maintains its due proportion. The fibres from the heart to the diabetic centre are conveyed in the vagus, and it is easy to see that on this theory the heart, which is the most active muscle in the body, may regulate the production of the material which furnishes it with energy.

Recent work by Mellanby locates a glycæmic centre in the brain, somewhere between the cerebrum and spinal cord. This centre is discharged by impulses passing to it by any afferent nerve, and is inhibited by impulses from the cerebrum.

In distinction to the above, which may be termed the ' nervous theory of sugar liberation,' we have another, the chemical, based upon the knowledge which exists of the glycosuria which results from depriving an animal of its pancreas. In some way or other which is not known, the pancreatic tissue is intimately connected with this sugar question, and this can be explained on the supposition of an *internal secretion*, which prevents the blood from becoming overloaded with sugar, either by regulating the amount which is liberated from the liver, or by stimulating the sugar-splitting action of the tissue-cells. It would on this basis be reasonable to suppose that the pancreatic extract should yield a glycolytic substance, but no such has been found. That the visible pancreatic secretion takes no share in the process is evident from what has been previously stated—viz., that if only a fragment of pancreas is left behind in the body of a depancreated animal no glycosuria results.

An extract of pancreas, it has been stated above, has no glycolytic power; further, an extract of muscle has no sugar-destroying power, but if the extracts be mixed glycolysis results. From this it has been supposed that the pancreatic extract activates a sugar-destroying enzyme present in muscle, which enables the latter, under physiological conditions, to oxidise sugar in the body, and obtain from it heat and energy. The activating substance furnished by the pancreatic extract is not an enzyme, for if the extract be boiled the substance is not destroyed; it is therefore assumed that the internal secretion of the pancreas is a *hormone* (see pp. 197, 260). There are others who consider that the function of the internal secretion is not to furnish the tissues with the power to metabolise sugar, but rather to regulate its output from the liver, and that when this regulation fails diabetes results, owing to the excess of sugar in the blood. The balance of evidence, however, suggests that the defect lies in the inability of the tissues—especially the muscular—to oxidise the sugar brought to them. The question is still, however, *sub judice*.

The pancreas in structure resembles the salivary glands in being of compound tubular type, but in it may be seen with the naked eye spherical or oval bodies, which are obviously not ordinary pancreatic tissue; these are known as the *Islands of Langerhans*. The islands are composed of groups of cells, each group surrounded by a rich capillary network of bloodvessels, and the view has been advanced that they are the seat of the production of the internal secretion. Ligature of the pancreatic duct causes the ordinary gland tissue to atrophy, but does not affect the islands, nor does ligature produce glycosuria. This is evidence in favour of their furnishing the internal secretion. There are other observers who consider the islands are concerned in the production of the ordinary pancreatic secretion. This latter view may now be regarded as disproved.

Diabetes.—In the forms of glycosuria hitherto described, its production has been experimental. But there is a pathological condition in which much the same symptoms are present; though, so far as we know, the herbivora do not suffer from this disease, it has been described in the dog, and under any circumstances its features in man are of interest to us. In diabetes the sugar in the blood, instead of being 0·1 per cent., as it normally is in man, may rise to 0·4, or even as high as 0·7 or 1 per cent. In consequence of the tissues being unable to consume the dextrose brought to them, the sugar passes off by the urine, and the body is starved of its source of heat and energy. As the disease advances, not only sugar, but products of deranged protein and fat metabolism, appear in the urine, such as *acetone*, *aceto-acetic acid*, and *oxybutyric* acids. These acids, by combining with the alkali of the blood, produce the condition known as *acidosis*, and reduce the carbon dioxide carrying capacity of the fluid; in consequence, the carbon dioxide accumulates in the tissues, and *diabetic coma* results.

Pathological.

The most common pathological condition of the liver is **Jaundice,** and the majority of, if not all, cases of jaundice are obstructive—*i.e.*, there is some obstruction to the free pouring out of bile; in consequence, there is a backward pressure, which, being greater than the low blood-pressure under which bile is secreted, causes the bile to be reabsorbed, and consequently stains the tissues yellow. There is also a form of jaundice affecting the horse and the dog, due to a parasite in the blood; in these cases the yellow tint is derived from the destruction of red corpuscles stimulating the production of bile (see pp. 8, 29). **Biliary Calculi,** consisting largely of the calcium salt of bilirubin, are not uncommon in ruminants and swine, but rare in the horse. **Fatty Liver** is common in all animals overfed and underworked. In the horse it may lead to **Rupture** of the liver during work. **Enlargement** of the liver is very common as the result of vascular disturbance elsewhere; it is not uncommon as a sequel to pneumonia, strangles, and other prolonged febrile changes. **Abscess** of the liver is rare, but not unknown. **Parasitic** disease of the liver is one of the epizootic diseases of sheep, and is common in the ox, but rare in the horse. The parasite occupies the bile-ducts, which become practically occluded.

In India, **Calcareous Degeneration** of the liver is one of the most common affections of this organ, and throughout the tropics generally liver disorders are very frequent. In South Africa **Hepatitis** occurs in horses as the result of eating "ragwort" (*Senecio Jacobaea*).

The pancreas is seldom the seat of pathological disturbances; it may be affected with abscess in strangles or in septic diseases, but such conditions are unrecognisable during life.

Sugar in urine is described as occurring in dogs; we have never met with it in horses, though *polyuria* is a common affection. On the other hand, many physiologists have described hyperglycæmia and glycosuria in animals as occurring under the influence of certain narcotics and anæsthetics.

CHAPTER VII

ABSORPTION

Section I.

Lymph.

Lymph may be regarded as the material by which the tissues are directly nourished, and by which effete material is collected from them and taken back to the blood; there are certain non-vascular structures, such as the cornea, cartilage, etc., where the lymph circulation is the only means by which the part is supplied with nourishment. Speaking generally, the lymphatic system may be described as the drainage system of the body, in contradistinction to the blood or irrigating system, though the latter is not exclusively devoted to irrigating, for it may also take up material from the tissue spaces.

The Lymph Spaces.—The tissues are bathed in lymph, which is contained in the lymphatic spaces existing between the capillary bloodvessels and the capillary lymph-vessels. There is a constant passage of material from the blood into the tissues, from the tissues into the lymph, and likewise from the tissues back to the blood.

The lymph spaces are irregular passages in the connective tissue, the larger ones being lined by epithelioid plates of peculiar irregular outline; these spaces exist outside the bloodvessels, and the lymph finds its way from the bloodvessels into the lymph spaces. From the lymph spaces the fluid reaches the lymph capillaries, but the means by which it gets there is not clear, for it appears certain that, excepting in a few cases, there is no direct communication between the space and the capillary. In the vessels of the brain a peculiar arrangement is present; the lymphatic vessels surround the artery, and obtain their lymph direct; these are known as perivascular lymphatics. The lining of the **Lymph Capillary** is composed of the same epithelioid plates with irregular outline which are found in the spaces, and it is believed that at the junction of the plates, crevices or intervals may exist through which fluid may find its way by the simple process of transudation. From the lymph capillary begins the **Lymphatic Vessel,** which, in addition to an epithelioid lining, has also a muscular coat, more marked in the large than in the small vessels, and also a connective-tissue covering. In the interior of these vessels valves are found which are essentially similar in structure, arrangement, and mode of action to those in the veins. Immediately beyond each valve there is a dilatation of the vessel which gives it a beaded appearance when the lymphatic is distended.

The whole of the lymphatics of the body converge towards a central vessel, the thoracic duct; those from the left side of the head and neck, the left fore-limb, the chest, abdominal cavity, and hind-limbs, join the duct at different points, and this in turn opens into the anterior vena cava; from the right side of the head and neck, and right fore-limb, the lymph vessels collect and pour their contents by a separate duct into the same vein. The thoracic duct is nothing more than a large lymphatic vessel, possessing the same structure as the lymphatic vessels above described, the muscular coat being especially well marked. The thoracic duct receives the lymph, not only from the ordinary tissues, but also from the intestinal canal. During starvation the mesenteric lacteal vessels convey to the duct a fluid which is essentially lymph, but during digestion this clear fluid is replaced by a turbid white fluid known as chyle; at this period the lacteal vessels are carrying not only lymph, but also the products of digestion, the milkiness of the chyle being due to the presence of emulsified fats.

The **Serous Cavities** of the pleura, pericardium, and peritoneum, have been looked upon as large lymphatic spaces, though this is now considered doubtful. Yet the fluid they contain is lymph, and they are in direct communication with lymphatic vessels, especially those of the diaphragm. In the diaphragm slits or stomata exist, and into these the lymph readily finds its way, being aspirated into the vessels during the respiratory movements of this organ; so readily is this effected that the diaphragm may be injected in a recently dead subject, by placing some milk on its surface and establishing artificial respiration.

The lymphatic vessels in their course pass through bodies known as **Lymphatic Glands,** entering at one side and emerging at the other. Experience shows that in its passage through these glands the lymph has corpuscles added to it which ultimately become white blood-corpuscles, and, moreover, it acquires the property of clotting. The gland consists of a *capsule,* within which is a mass of adenoid tissue divisible into a *cortex* and *medulla*. The capsule sends in bands of tissue (*trabeculæ*) which divide the gland into compartments or *alveoli*, those in the cortex being much larger than those in the medulla. The alveoli contain a network of connective tissue, whose central part is finely meshed (*adenoid tissue*), closely packed with lymph corpuscles, and constitutes the *glandular substance*. The adenoid

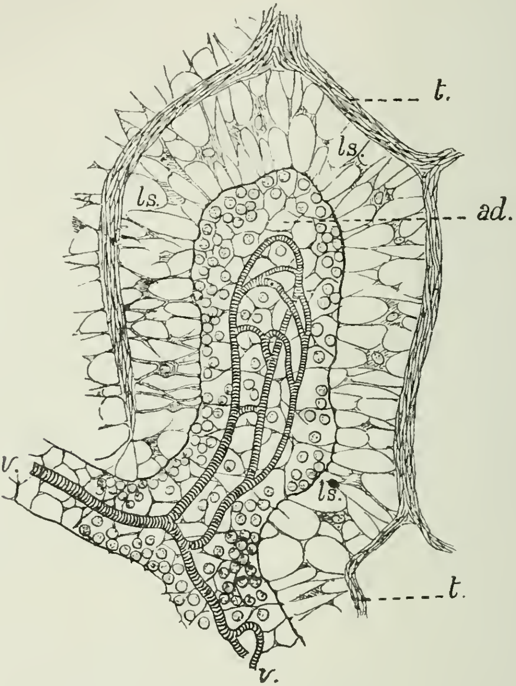


FIG. 84.—DIAGRAMMATIC SECTION OF LYMPHATIC GLAND.

ad, Adenoid tissue containing lymph corpuscles. The region *ad* is normally densely packed with lymph corpuscles, and constitutes the glandular substance. The corpuscles are here drawn in scanty numbers, so as not to obscure the central capillary *v*. In the adenoid tissue may be seen a capillary bloodvessel *v*. Outside the core of adenoid tissue is the lymph sinus or space *ls*, across which run branched nucleated corpuscles which form simply an open network of connective tissue. Surrounding the whole is the trabecular framework *t*.

tissue does not occupy the entire alveolus, but fills up the centre, and is maintained in position by branched, nucleated, connective tissue corpuscles passing to the wall of the alveolus. In this way a space or channel is formed between the central mass of adenoid tissue and the wall of the alveolus; this channel is known as a *lymph sinus* (see Fig. 84). It is through the lymph sinuses of the cortex that the gland is in direct communication with the afferent lymphatic vessels. In the adenoid tissue of the alveolus there is a network of bloodvessels; the tissue itself is filled with corpuscles known as leucocytes, which are also found in the more open network extending across the lymph sinus. The medulla of the gland presents no essential difference in structure to that of the cortex, excepting that the reticular network is more complex, closer, and more extensive. The efferent lymphatic vessels originate in the lymph sinuses of the medulla.

Lymph is a slightly yellow-coloured fluid, alkaline in reaction, with a specific gravity of 1·012 to 1·022, and possessing the power of spontaneous clotting. The clot it yields is not so firm as that of blood, and takes longer to form; moreover, the bulk of fibrin is much smaller. Lymph may be regarded essentially as blood minus the red corpuscles; it contains, therefore, the proteins of that fluid—viz., fibrinogen, paraglobulin, and serum albumin, though in smaller amounts, also cells resembling the white cells of the blood, extractives, salts, and gases. The fluid in which these are contained is spoken of as lymph plasma. The gases consist principally of carbon dioxide, the amount of which is greater than in arterial, but approximately the same as in venous blood, a small quantity of nitrogen, and only traces of oxygen. Amongst the extractives some observers have found urea, a substance which exists more largely in lymph than in blood, and which is said to be always present in the lymph of the cow. The salts are distributed much as are those in blood—viz., potash in the corpuscles, and soda in the plasma. It is evident that the composition of the lymph cannot be uniform, but must depend, among other causes, upon the nature of the food-supply and the source of the lymph.

The lymph-cells or leucocytes exhibit amœboid movements, and are identical with white blood-cells; they are more numerous in those vessels which have passed through lymphatic glands, for it is in the gland that the leucocytes are manufactured and added to the lymph. The cells consist of proteins, lecithin, cholesterin, and fat, and their nuclei contain nuclein. The proportion of lymph-cells to lymph is about the same as the proportion of white corpuscles to blood.

The Quantity of Lymph in the Body is difficult to determine, and varies considerably. From a lymphatic vessel in the neck of the horse Colin obtained ½ to 2 kilogrammes (17 to 70 ounces) in twenty-four hours; but the variations were wide. Colin noticed that the herbivora secrete more lymph than the carnivora, and young animals more than adults. From the thoracic duct of a cow this observer obtained the prodigious quantity of 91 kilogrammes (20 gallons) in twenty-four hours. This, of course, is no guide to the amount of lymph in the body, as the thoracic duct contains a mixture of body lymph and chyle from the intestines. In the observation mentioned on the cow the amount of material collected from the duct was more than double the blood in the body; and if, as is usual, we regard two-thirds of the contents of the thoracic duct flow to represent chyle and one-third lymph, it still leaves the lymph flow at a very high figure—in fact, nearly equalling the entire blood-content of the body. As a matter of fact, the total quantity of lymph in the body is unknown; it has been supposed that it may be two, or even three, times greater than that of the blood.

In the following table from Colin the amount of mixed chyle and lymph flowing from the thoracic duct was measured; the minimum represents a period of comparative digestive quiescence; the maximum amounts represent digestive activity.

Horse	-	14 to 40	kilogrammes	(24 to 70 pints) in 24 hours.
Ox	-	20 to 91	,,	(35 to 160 pints) in 24 hours.
Sheep	-	3 to 9·5	,,	(5 to 16 pints) in 24 hours.
Dog	-	1·3 to 2·6	,,	(2·3 to 4·5 pints) in 24 hours.

Formation of Lymph.—The method by which lymph is formed has been the subject of great difference of opinion and of innumerable experiments. The question is still unsettled, so that it is necessary to present both views of the case. The difficulty in explaining the production of lymph lies in the fact that the systems of bloodvessels and of lymph-vessels do not communicate; both, in fact, are closed systems, while between them lie the tissue spaces. What has to be explained is the passage of fluid from one to the other across this space. If secretory nerves for lymph production had a definite existence, all difficulties would disappear; but though the existence of these has been suspected, and by some even described, the balance of evidence is against their presence. But even quite apart from the existence of a special nervous mechanism, there are other grounds on which the theory of lymph formation could easily be explained—viz., on a physical basis, as of filtration, or diffusion; but, unfortunately, these processes frequently fail, under experimental inquiry, to behave in the living body as they do in the dead cell, though, in spite of this, physical processes have been, and continue to be, invoked in explanation in those cases where their action is not negatived by experimental results. Finally, the explanation of the selective action of the living tissue-cells has been urged as the real explanation of the phenomenon. As a matter of fact, it is no explanation, though it may, and probably does, tell us something of what is occurring, or fixes on the means by which it is taking place. Nevertheless, if the cell could be proved to be the factor in lymph formation, this would make a substantial addition to our knowledge of the subject; the difficulty of explaining the selective power of the cell which secretes lymph is only the same difficulty which exists in considering the cell which secretes urine, or bile, or sweat. The nervous mechanism, of which there is so little evidence, being put aside entirely, the two chief theories of lymph formation resolve themselves into the physical and secretory, and each of these must be examined separately.

The **Physical Theory** is based upon a knowledge of the laws governing filtration, diffusion, and osmosis, and was first applied by Ludwig.

Two liquids miscible, but utterly unlike, if brought into contact, will gradually form a homogeneous mixture as the result of diffusion. If they be separated by a membrane permeable to their molecules, diffusion will occur through this, and a mixture of uniform composition result. Diffusion through a membrane is known as osmosis. Substances which are diffusible are known as crystalloids, those which are non-diffusible are called colloids. Sugar or salt are good examples of diffusible bodies, proteins and starch are examples of colloids, the large size of the molecules of the latter preventing their passage through an animal or other membrane. This difference in the behaviour of these two classes of substance, as regards their osmotic properties, affords a useful and ready means, known as *dialysis*, of separating the crystalloids from the *colloids*.

If two masses of water be separated by a membrane, the diffusibility of each being equal, as many molecules will pass into one chamber as enter into the opposite, though to all appearances no change in the fluid is taking place. If one chamber contains salt solution and the other plain water, it will be found that much more water passes into the salt solution than salt solution into the water, the rate of transference of the salt depending upon the concentration of the salt solution; the force which brings this about is known as the *osmotic pressure*. It can be shown that the osmotic pressure is proportional to the number of molecules of the crystalloid in solution.

Filtration is the passage of fluid through a membrane as the result of pressure. If the pressure of blood in the capillaries could be shown to be higher than the pressure in the lymph vessels or spaces, adequate ground would exist for regarding filtration as an agent in lymph production. As a matter of fact, the pressure in the lymph spaces is unknown, and the pressure in the lymph capillaries is unknown; but there is the best of reasons for believing that the pressure falls from the blood capillaries to the lymph capillaries, and by increasing the pressure in the former—say, by tying or compressing a vein—œdema results in consequence of the filtration of fluid from blood capillary to tissue space. The fluid in the tissue space may or may not be lymph as we find it in a lymphatic vessel. The plasma has passed through the wall of one vessel and become altered in composition; in the tissue space it is certain that further change in its composition occurs in consequence of tissue activity, and another vessel wall has to be negotiated before the lymph stream is reached; this passage may occasion further change in its nature. The question of the actual changes in the composition of the lymph in its passage from blood capillary to lymph capillary does not immediately concern us here, but it helps to explain why some physiologists have such difficulty in accepting purely physical reasoning where living tissues are concerned, even when the process concerned is as simple as that of filtration. Nor must it be considered that the presence of an increase of pressure in the capillaries necessarily results in the formation of more lymph. In the horse it has been shown that the flow of lymph from the parotid gland is not appreciably increased when the gland passes from a condition of rest to that of secretory activity, and yet we know that the capillary pressure at the time is greatly increased. Other evidence will be quoted later showing that serum may be absorbed from the bowel when the pressure in the capillaries is greater than the pressure in the intestines; it may be urged that the case of the bowel and bloodvessel is not comparable with that of the tissue space and bloodvessel, but our object is rather to show that filtration may be non-existent at the moment when the necessary physical conditions for its activity are present. It has been shown, therefore, that there are features in lymph formation which cannot be entirely explained on the theory of filtration.

Diffusion and Osmosis.—For many years it has been known that if two fluids—one containing salt, and the other pure water—be separated by a membrane of parchment, one passes into the other through the pores of the membrane, until the same amount of salt exists on both sides of the diaphragm. Fluids which thus pass through are termed **crystalloids**; those which refuse to pass through are known as **colloids**; while the entire process is termed **osmosis** or **dialysis.** We shall see presently that physical chemistry of the present day gives a more restricted definition to the term 'osmosis.'

It is known that perfectly pure water is not a conductor of electricity, and the same may be said of solutions of sugar, urea, albumin, and other bodies. The explanation afforded by modern chemistry is that the molecules of pure water and the molecules of sugar undergo no *dissociation* into their constituent *ions*. Substances which dissolve in water and undergo dissociation are conductors of electricity. For instance, sodium chloride is broken up in water into sodium *ions* and chlorine *ions*, each group being charged with an opposite form of electricity, the sodium ions being positively, the chlorine ions negatively, charged.

Substances so capable of dissociation are termed *electrolytes*, and their interest to us at the present time is in connection with osmosis;

the act of dissociation liberates a number of ions, and by so doing increases the number of particles moving in the fluid. It can be shown that osmotic pressure—a term yet to be explained—is proportional to the number of molecules of dissolved substances present, and in the above example the ion behaves as a molecule in osmotic pressure. Generally speaking, the greater the dilution, the larger the number of ions dissociated.

Though not directly connected with the matter under consideration, it is convenient in this place to look at the part played by *ionic* action in the body. It is by a due adjustment of ions in their surroundings that the contractile tissues which work in a saline artificial circulation (p. 52), are capable of so doing; and the same may be said of cilia, of amœboid action, etc., each of which requires its own definite proportion of ions. Loeb has classified the ions responsible for rhythmic contractions, though such a classification can at present be regarded only as provisional. So much importance does this observer attach to ionic action that he has brought forward evidence to show that fertilisation of the ovum may be ionic in its nature, the spermatozoa merely regulating the proportion of ions. Even a nerve impulse he regards as depending on an electrolytic action.

Osmotic Pressure.—If a solution of an electrolyte such as common salt be enclosed in a specially prepared semi-permeable cell, water will pass in, but salt will not pass out, either by filtration or by diffusion. This can be proved by placing the cell in distilled water, and if a manometer be connected with the cell it will be found that as the water passes in the pressure increases. This pressure is known as osmotic pressure, and the term ‘osmosis’ at the present day is confined to the stream of water passing through a membrane, while ‘dialysis’ is restricted to the passage of the molecules dissolved in water. In the above experiment it will be found that, if the strength of the salt solution be doubled, the manometer will indicate twice the pressure, so that the amount of osmotic pressure is always proportional to the number of molecules of the dissolved substance in a given volume of the solution.

The nature of osmotic pressure is unknown; it can be shown to be independent of the nature of the substance in solution, and proportional to the number of molecules of the dissolved substance. It is governed by laws closely analogous to those governing gaseous pressure, and, like gaseous pressure, it is affected by variations of temperature and by the law of partial pressure. The latter, in the case of osmotic pressure, is expressed by saying that the osmotic pressure of a solution of different substances is equal to the sum of the pressure which the individual substances would exert if they were alone in the solution. Osmotic pressure is conveniently estimated by ascertaining the freezing-point of a substance soluble in water, which is always lower than that of the water itself; the lowering of the freezing-point is proportional to the molecular concentration of the dissolved substance, and this molecular concentration is proportional to osmotic pressure. Sugar, for instance, not being an electrolyte, has a smaller number of particles moving in the solution than sodium chloride, which is capable of dissociation, so that the osmotic pressure of salt is higher than that of sugar. A 1 per cent. solution of sugar has an osmotic pressure of 473 mm. mercury, while 0·9 per cent. of common salt, which has the same osmotic pressure as blood-serum, exerts a pressure of 5,000 mm. mercury.

Blood-serum is taken as the standard in physiological inquiry;

any solution which has the same molecular concentration as serum, and consequently exerts the same osmotic pressure, is termed **isotonic** ; if it has a greater osmotic pressure, it is termed **hypertonic**; and if less, **hypotonic.** For example, on p. 8 the action of salt solution on red corpuscles has been described; if the addition of a solution causes no effect, it may be known that it is isotonic to the material within the corpuscles; if it causes the corpuscles to shrink and become crenated, it has a greater osmotic pressure than the cells, and is hypertonic; if it causes them to swell and discharge their pigment, it has a smaller osmotic pressure, and is hypotonic.

It is not difficult to see how the physical factors of osmotic pressure and diffusion may be turned to account in explaining the formation of lymph, absorption from the intestines, secretion of urine, and such-like processes. The danger, as has been previously indicated, lies in their uncompromising application, and in the liability to forget that the living body is neither a parchment membrane nor a vessel with a semi-permeable lining. It has been urged that it is impossible to disregard the value of osmotic currents in restoring equilibrium of composition between the blood and the tissues or the tissues and the blood; for example, if a strong solution of common salt be injected into the blood-stream, a current is created from the tissues into the blood, by which the tissues may lose water; but later on diffusion will come into play, and the tissues will draw water from the blood. It is suggested that constant and rapid osmotic changes are occurring between the blood and the tissues; so rapid, indeed, may these be that if the osmotic equilibrium be upset by injecting a large dose of dextrose, within half a minute it is readjusted. We have seen that the lymph in the spaces must necessarily be undergoing constant change in its composition and concentration, as the result of tissue activity, with its attendant chemical changes. It is, therefore, readily conceivable that osmotic or diffusion currents may be set up, water being drawn from the blood to the tissue spaces and crystalloid bodies, such as would result from the breaking up of the protein molecule, passing by diffusion from tissue spaces to blood, and so being got rid of by the excretory organs; of such crystalloids the precursors of urea are a good example.

Experimental inquiry, however, shows that it is not easy to explain lymph formation by osmosis or by diffusion, and we have previously seen how greatly filtration has failed. The injection into a vein of a strong solution of common salt, urea, or dextrose, is followed by an immediate *increase* of lymph; whereas the osmotic pressure exerted by sodium chloride, for example, should at least primarily diminish the secretion by setting up osmotic currents from tissues to bloodvessel, although, secondarily, the hydræmic plethora should give rise to increased filtration from the blood. Even as regards the subject of absorption, which it is difficult to divorce from that of lymph formation, osmotic pressure does not help as much as might be expected. Again, it can be shown experimentally that there is no definite relation between the rate at which the sugars are absorbed and the osmotic pressure they exert. Serum, isotonic with blood-plasma, may be absorbed from a loop of intestine, when the blood-pressure in the capillaries of the intestine is greater than the pressure within the bowel. Evidently in this case osmotic pressure cannot have been exercised, while absorption by filtration is negatived by the higher pressure in the capillaries. Salt solution, isotonic with blood-plasma, may also be readily absorbed by the blood-vessels in the peritoneal cavity. In all these cases something is occurring which is opposed to what might have been expected from a purely physical reasoning. But perhaps few things are more remarkable in this respect, or more difficult to explain, than the effect of the injection of dextrose, which causes a *post-mortem flow of lymph* for as long as an hour after the circulation has ceased. Whether the question be considered from its physical or secretory aspect, this post-mortem flow is inexplicable.

Indiffusible substances such as protein are believed to exert but little osmotic pressure, and some consider none whatever. The large size of the protein molecule, and the small number (6 or 7 per cent.) present in such concentration, as is represented by blood-serum, explains why they exert little or no pressure. The passage of protein through the capillary wall to the lymph vessel cannot be satisfactorily explained by osmotic pressure; a filtration has consequently been assumed to be the agent at work, as the blood in its capillaries is at a higher pressure than the lymph in its capillaries.

Starling, whose name is so closely identified with the investigation of lymph production from its physical aspect, has laid stress on the importance of the permeability of the capillary wall. His observations show that the normal undamaged capillary of the limbs and connective tissue offers a very considerable resistance to the filtration of lymph, and keeps back a large portion of the proteins of the blood-plasma; on the other hand, the intestinal capillaries, and especially the capillaries of the liver, are very permeable; a very small capillary pressure in the latter suffices to produce a large transudation of lymph containing as much protein as the plasma itself. A normally impermeable capillary of a limb may by injury be at once converted into a permeable capillary, within which the slightest increase in pressure brings about lymph production.

Starling records the remarkable fact that no lymph can be obtained from a *resting* limb, though active or passive movements of it at once cause a flow of lymph. The only part of the body which produces a continuous flow of lymph during rest is the alimentary canal. Though no lymph is yielded by a resting limb, yet the chemical changes in the tissue are still occurring, oxygen is being absorbed and carbonic acid and other waste products got rid of, but their channel of excretion is meanwhile the bloodvessels.

The Secretory Theory of lymph formation is based on a knowledge of the secretory activity of epithelium in general. It was natural to regard the endothelial lining of the capillary vessels as the possible seat of secretory activity, as was known to be the case in other tissues; and when Heidenhain was able to show that by the injection of certain substances into the blood he was able to increase the flow of lymph without increasing the arterial pressure, it appeared that the solution of the vexed question of lymph formation was at hand.

Heidenhain found that the injection into the blood of peptone, extracts of leech, crayfish, mussel, egg-albumin, etc., increased the rate of lymph flow, and also the total solids in the lymph obtained from the thoracic duct. He called these substances **lymphagogues,** and divided them into two classes, the first class consisting of such substances as the above, while the second consisted mainly of crystalloid bodies such as sugar and salt, which, though increasing the total quantity of lymph produced, rendered it more watery than usual.

As regards Class I, Heidenhain believed they contained a specific substance which stimulated secretion. Starling showed that the increased secretion was derived from the liver; he believed the extracts acted pathologically on the walls of the blood capillaries of the gland, and rendered them more permeable; hence the increased flow of lymph. The second class of lymphagogues was believed by Heidenhain to act by attracting water from the tissues, and so increasing the bulk of lymph. Starling, however, maintains that in this case they act by increasing the osmotic pressure of the circulation, so that water from lymph and tissues is attracted into the blood by osmosis. The excess of fluid thus produced in the blood causes a rise in the capillary pressure, especially in that of the abdominal area, followed by increased transudation from the capillaries into the lymph vessels.

At present it is not possible to decide between the rival theories of lymph formation; it may be proved that under given conditions both methods take a part in the process of secretion. It seems impossible to exclude the living activity of the cell-body, so strongly emphasised in the consideration of other secretions, while it is equally certain that there are other conditions which are possible of explanation only on a physical basis.

The **Movement of Lymph** is effected largely by muscular contractions in the neighbourhood of the vessels, by which means the vessels are themselves compressed and their contents forced onwards, since the valves which they contain prevent a back flow. The obstruction caused by the lymphatics passing through glands is not serious, while the involuntary muscle fibres in the capsule of the gland more than compensate by their contraction for any resistance in the gland itself. The pressure of the lymph in the lymph vessel is higher than that in the jugular vein, so the flow of lymph from the tissues to the vein is assisted by the fact that the fluid is passing from a region of higher to one of lower pressure. The movements of the diaphragm, tendons, and fasciæ produce an aspirating effect on the lymph circulating through them. In the diaphragm the lymphatic vessels drain the two large lymphatic sacs the pleura and peritoneum; owing to the direction taken by the fibres of the diaphragm, compression is exerted on the lymph spaces during its contraction, while a sucking action is produced when it relaxes. This pumping arrangement exists in tendons fasciæ of muscles, etc., and is a valuable aid to lymph circulation. In the ordinary skeletal muscles during contraction the lymph is squeezed out of the part by compression. During rest practically no lymph passes by the lymph vessels of muscle, the exchange taking place, as we have seen, by the bloodvessels.

Once the lymph from the abdominal viscera and hind-quarters has found its way into the thoracic duct, its passage into the general circulation is favoured y gravity, by the muscular contraction of the coats of the duct, and by movements of the skeletal muscles, especially the abdominal. The lymph from the right side of the face neck, and right thorax has a duct of its own, and this is so situated that gravity plays an important part in moving the contents along. Both the thoracic duct and the right lymphatic duct empty into the veins near the heart, either into the anterior vena cava or into the jugular confluent. The mode of entry varies; in fact, there are great variations in animals of the same species, in the anatomical arrangements, not only of the ducts, but also of their terminations; for example, the thoracic duct is frequently duplicated in the ox.

In whatever way connection with the venous system is made, a valvular arrangement, looking towards the vein, and intended to prevent a reflux of blood into the duct, exists between the dilated termination of the lymph duct and the bloodvessel. This valvular seal is a reliable one in the ruminant; in the carnivora it is less so; in the horse it is imperfect, so much so that blood may find its way even for some distance into the duct, and stain the contents, as first pointed out by Colin. If a manometer tube be placed in the thoracic duct of the ox at its termination in the vein, the mixed contents of chyle and lymph will rise in the tube, and in about five minutes reach a maximum. The amount of this is variable; Colin has registered during full digestion a 3-foot pressure (say 75 mm. mercury) in the thoracic duct, which is about one-third of the aortic pressure. This is very high—indeed, is higher than that of the blood in the capillaries or of the lymph in the lymph vessels. It would appear that this marked degree of pressure can be due only to contraction of the walls of the *receptaculum chyli* and contraction of skeletal muscles, the abdominal muscles doubtless taking the largest part therein. The fluid in the tube rises and falls, and if the tube be removed lymph issues from the vessel in jets. The rise and fall of level in the tube is associated with respiratory movements, but the effect produced is not the same as the general effect on blood-pressure caused by inspiration and expiration. Inspiration does not, for instance, draw the lymph from the duct towards the vein—its effect is the reverse; while expiration, on the other hand, raises the pressure in the duct, and discharges its contents. Colin, who first described this singular fact, explains it by saying that the intrathoracic pressure being reduced during inspiration, the vessel dilates, and, in consequence, its capacity is increased. During inspiration it fills up, while at expiration the pressure exercised upon it, no doubt particularly by the abdominal muscles, causes the now distended duct to discharge its contents. Colin, in fact, observed that the oscillations of the fluid in the manometer tube are greater during laboured respiration. In the horse the pressure in the thoracic duct must be much less than in the duct of the ox; in fact, for blood to pass into the duct the pressure must be at times below that of the pressure in the anterior vena cava. There are great experimental difficulties in getting at the duct in the horse, and exact information is wanting.

The lymph moves slowly in its vessels. Weiss has observed a rate of from 230 to 280 mm. (9 to 11 inches) per minute in a large lymphatic in the neck of the horse, but the velocity in the small vessels is very much less. Colin observed 120 mm. (4¾ inches) per minute. The flow from the thoracic duct of a calf was found by Colin to be 1 metre (3 feet 3 inches) a minute; in a large mesenteric vessel the same observer found the velocity to be 840 mm. (33 inches) a minute.

As fast as the lymph finds its way from the bloodvessels into the spaces it is normally passed on to the lymphatic capillaries, so that the rate of output is equivalent to the rate of removal; when, however, the output is greater than the rate of removal the lymph accumulates in the tissues, and **Œdema** results. It is conceivable that the rate of removal need not necessarily always be at fault, but that the rate of secretion may be so greatly increased that the outgoing channels are unequal to the demands made upon them. In such an increased secretion of lymph the defect lies in the vascular system, and experience shows that increased formation of lymph is a more common cause of œdema than defective drainage. It is well known that interference with the venous circulation is productive of œdema, the explanation being that not only is there an increase of pressure in the capillaries as the result of the venous obstruction, but also the venous blood is kept in contact with the wall of the capillary, and this induces changes in the epithelioid cells resulting in increased lymph formation. The swollen legs, so common in horses kept idle in the stable, are due to this cause. The venous blood ascends the limbs against gravity, and exerts on the capillaries of the legs below the knees and hocks a pressure which is nearly equivalent to the height of the vein; as a result, the cells of the capillary wall are the seat of an increased exudation, and the legs accordingly 'fill,' a condition at once removable by exercise. The pressure in a lymph vessel is low; in the neck of the horse it was found to be from ½ to ¾ inch of a weak solution of soda; in the dog the lateral pressure was half that found in the horse.

Hæmolymph Glands.—These are found in the ox and sheep, but are believed to be absent in the horse. They are of a deep red colour; the cortical and medullary substances are not sharply defined, and involuntary muscle is found in the trabeculæ. These glands occur among the gastric and mesenteric lymph glands, along the course of the aorta, in the perineal fat, and externally under the skin of the flank and under the trapezius muscle. Some possess afferent and efferent vessels, others do not. The significance of these glands is unknown. (Sisson.)

SECTION 2.

Chyle.

In the thoracic duct the lymph from the body meets with the lymph coming from the intestines, termed ‘chyle.’ This chyle is derived from the villi, and passes up the mesentery by many vessels, which in the horse are said by Colin to number 1,200. Each of these passes through a lymphatic gland before entering the *receptaculum chyli.* Chyle is closely allied to lymph in its chemical composition, but it differs from it in containing a quantity of neutral fat, taken up during intestinal digestion, which gives it a milky appearance. The amount of this fat in dogs may vary from 2 per cent. to 15 per cent., or even more. The fat is partly in the condition of measurably large droplets, such as are seen in milk, but for the most part it exists as extraordinarily minute particles; hence the name ‘molecular basis,’ which is applied collectively to the fat particles in chyle.

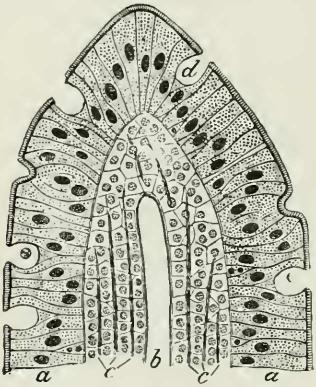
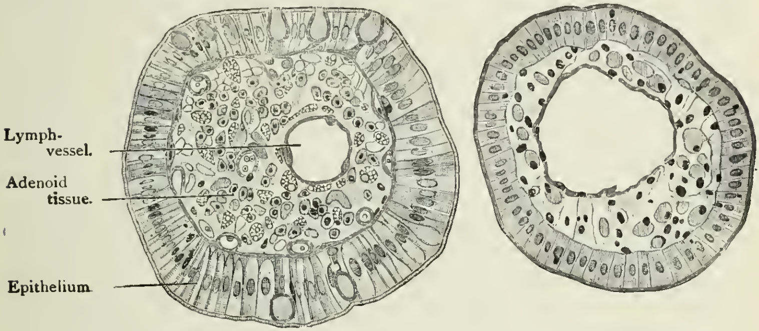


FIG. 85.—VERTICAL SECTION OF A VILLUS: CAT. × 300 (STEWART).

a, Layer of columnar epithelium covering the villus — the outer edge of the cells is striated; *b*, central lacteal of villus; *c*, unstriped muscular fibres; *d*, mucin-forming goblet cells.

The Villi.—We have mentioned that in the ordinary tissues the radicles of the lymph vessels are the lymph spaces, but in the wall of the small intestines the origins of the lymph vessels are highly differentiated structures, known as villi and solitary glands. The villi (Fig. 85) are innumerable projections from the inner surface of the mucous membrane shaped like minute fingers; they are found only in the small intestines, and have been calculated by Colin to amount to forty or fifty millions in the horse and in the ox. In the interior and central part of the villus is a vessel termed the *lacteal;* it may be single or multiple, straight or branched, and at the base of the villus it opens by a valvular arrangement into the lymphatic system. Surrounding the lacteal is a network of capillary bloodvessels, while filling up the finger of the villus, where not otherwise occupied by vessels, is a peculiar structure found especially in lymphatic glands, and known as adenoid tissue (p. 275); this tissue is relatively larger in amount in the villi of carnivora than of herbivora (Fig. 86). Covering the adenoid tissue is a basement membrane on which is set a layer of columnar cells, placed so that their narrowest end is next the basement membrane, and their broadest at the surface of the villus. The cells at their narrowest part are in touch with the adenoid tissue of the villus. Each cell contains a nucleus, and on that edge of the villus, next the interior of the bowel, is a clear band bearing fine striations. Lying between the columnar cells are others which from their shape are spoken of as 'goblet cells' (Fig. 86); by means of a pore they extrude their contents, consisting of a transparent material known as mucin, into the intestine. Within the villus are bands of involuntary muscle fibre arranged parallel to the axis of the villus, by the contraction of which, combined with the peristaltic movements of the intestine, the capacity of the lacteal vessel is altered in such a way that it is alternately filled with lymph from the reticular adenoid tissue, and emptied of lymph into the lymphatic vessel at the base of the villus. This is known as the pumping action of the villus, and is an important factor in the conveyance of the chyle (lymph) towards the thoracic duct.



DOG. RABBIT.

FIG. 86.—TRANSVERSE SECTION OF VILLI OF CARNIVOROUS AND HERBIVOROUS ANIMALS (WALLER, AFTER HEIDENHAIN).

The large cells in the epithelial zone of the dog are the goblet cells.

The other lymph radicles found in the intestine are the *Solitary Follicles*, which are found studding the whole of the mucous membrane of the small intestines; these solitary follicles are, at certain places in the ileum, found as masses, which are known as *Peyer's Patches*.

The **Solitary Follicle** is essentially a lymphatic structure, and is not concerned like the villus in absorbing anything from the food. It consists of a mass of adenoid tissue, the network of which is filled with leucocytes; within the network are capillary bloodvessels, and surrounding the whole is a space across which branches of the adenoid network pass. This space is known as a *lymph space or sinus ;* it is lined, like those previously described, with epithelioid plates, and opens into a lymphatic vessel. As the lymph passes through the adenoid tissue, some of the corpuscles found in the meshes of the network are added to it, and become lymph corpuscles.

Chyle is a turbid fluid of alkaline reaction and a specific gravity of 1·007 to 1·022. In starving animals it is transparent owing to the absence of fat, and it is, in fact, at this time pure lymph. Colin observed that the chyle of herbivora was yellowish or yellowish-green; it is possible that this colour may be due to chlorophyll taken up from the food. In the horse, as collected from the thoracic duct, it is often blood-stained, due, as we have seen, to leakage from the vena cava.

In the small intestines of the horse it has been observed by Colin that almost immediately after food has been given waves of chyme are passed into the duodenum from the stomach; in consequence, the lacteals in the mesentery in connection with this portion of intestine become opaque, though previously they were filled with a colourless fluid. As the chyme passes along the bowel the other lacteals in their turn become opaque, until at last the whole of them are filled with this milky fluid (Fig. 87). Colin draws especial attention to this regular invasion of the lacteals from the duodenum to the ileum.

The movement of chyle is due to the rhythmical muscular contractions of the walls of the intestine, and to the muscular contraction of the intestinal villi forcing it onwards, while the valves in the lacteals prevent its return. Its subsequent passage into the general circulation has already been traced.

SECTION 3.

Absorption in General.

The activity of absorption, especially in the horse, has been made known to us by the experiments of Colin.

Absorption from the Respiratory Passages is remarkably rapid. Colin showed that potassium ferrocyanide could be detected in the blood two minutes after being injected into the trachea, and that it appeared in the blood before it was found in the chyle; the same salt was also found in the urine eight minutes after being introduced into the trachea. A solution of nux vomica injected into the trachea produced tetanic symptoms in three minutes; turpentine, alcohol, and ether were also rapidly absorbed, but oil could not be taken up, and was rejected by the nostrils.

Such drugs as morphia, pilocarpine, physostigmine, etc., are all rapidly absorbed from the air passages,* and produce their physiological effect in a shorter time than when simply injected under the skin. The lungs also have the power of absorbing certain poisons such as curare, which are not absorbed when introduced into the digestive canal. The absorption of water from the bronchial passages is very rapid. Colin introduced 6·8 litres (6 quarts) of water per hour into the trachea of a horse; the animal was destroyed at the end of three and a half hours, and no fluid was found in the bronchi. He also poured into the air passages 568 c.c. (1 pint) of water at a time; repeating this without intermission, he poured in 42 litres (74 pints) of water before he caused death. So rapid is absorption from the bronchi, that a horse may be placed under chloroform almost instantaneously by an intratracheal injection of the drug.† The rapidity of absorption is therefore very great, but in spite of the facility with which drugs are taken up, the lining membrane of the bronchial tubes is remarkably tolerant of such irritating agents as turpentine, strong liquid ammonia, acetic acid, etc., and offers in a state of health an almost impassable barrier to putrid organic infusions, or at any rate these do not appear to produce any local irritation when injected.

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* It is interesting to observe that the injection of liquids into the trachea (either high up, or as low as its bifurcation) excites the reflex act of swallowing, probably due to stimulation of the sensory fibres of the inferior laryngeal nerve.

† It is not intended here to recommend the intratracheal administration of chloroform, which is not only dangerous, but produces the greatest excitement in the patient.

Absorption from the Cellular Tissue is very active, and both bloodvessels and lymphatics take part in the process; ferrocyanide of potassium injected into the face has been detected in a carotid lymphatic in seven minutes. The rapidity of cellular tissue absorption is increased by muscular movement.

Absorption from the Conjunctiva is very pronounced for some drugs, such as atropine and for certain organic poisons, but there are other substances which are not absorbed so readily. Curare is not absorbed through the conjunctiva, and Colin could not infect horses with anthrax by placing anthrax blood and fluids in the conjunctival sac.

Absorption by the Skin, if the surface be unbroken, is as a rule slow even for those drugs which will pass through it, while there are many organic and inorganic substances which refuse to pass through the unbroken epidermis. Colin kept the lumbar region of a horse wet for five hours with a solution of ferrocyanide of potassium; the salt was detected in the urine in four and a half hours, although the skin was quite unbroken. A solution of nicotine is readily absorbed, and in horses poisoning both by it and arsenical preparations, unless properly diluted, may readily occur. In the dog absorption from the skin of such drugs as carbolic acid, even in a very diluted form, is rapid and frequently fatal. From a wound or abraded surface, absorption will occur rapidly with some agents, slowly with others. Colin placed a horse's foot with a wound on the coronet in a solution of ferrocyanide of potassium; in twenty minutes he detected the salt in a lymphatic of the thigh. In connection with absorption from a wounded surface, he found that the poison was taken up quite as readily by the lymphatics as by the bloodvessels. The mucous membrane of the vagina was found by experiment to absorb very slowly.

Experiments made on **Absorption from the Pleural and Peritoneal Cavities** showed that such drugs as strychnine rapidly produce fatal symptoms when injected into these sacs; even in such a short time as from three to seven minutes tetanic symptoms supervene. Potassium iodide injected into the peritoneal cavity of a sheep may be detected in the thoracic duct five to eight minutes after the operation. Starling and Tubby have shown, however, that the active agents in absorption from these sacs are the bloodvessels, and that the share taken by the lymphatics is insignificant; for if methylene blue be injected into the pleural cavity the dye appears in the urine long before any trace of colour can be perceived in the lymph flowing from the thoracic duct.

Stomach Absorption, or, rather, its absence in herbivora, has been dealt with at p. 207. Even in the dog it is now admitted that absorption from the stomach is by no means so certain as was at one time supposed. Water, for instance, passes through the stomach and undergoes no absorption; salts are absorbed only with difficulty; sugars and peptones are taken up, but only if in sufficient concentration; ordinarily they are absorbed with difficulty.

Intestinal Absorption.—The absence of stomach absorption in the horse and ox points to intestinal absorption as being of considerable importance in herbivora. That this absorption is very rapid is proved by Colin's experiments. Hydrocyanic acid injected into the small intestine of a horse caused death in one to one and a half minutes, and potassium ferrocyanide injected into the bowel, after the tying of the mesenteric lymphatics, was detected in the blood six minutes afterwards.

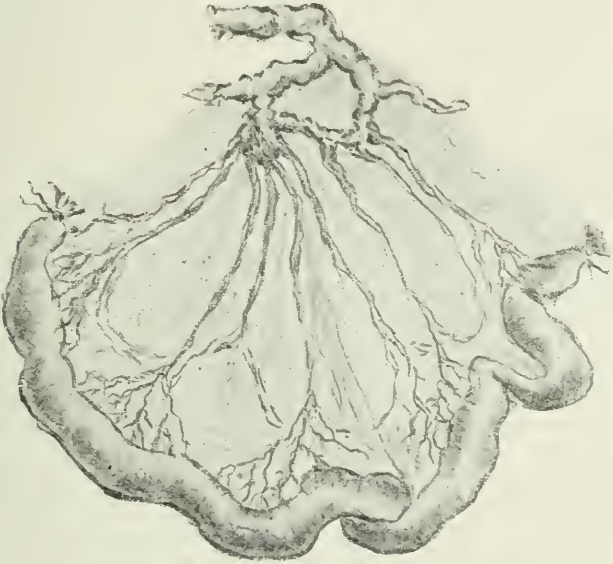

FIG. 87.—LOOP OF SMALL INTESTINE OF THE HORSE DURING ACTIVE ABSORPTION, WITH DISTENDED LACTEALS.

The Paths of Absorption.—The paths by which intestinal absorption occurs are (1) through the villi into the lacteals, and (2) through the bloodvessels into the venous system. This points to the fact that some substances taken up from the bowel may at once pass into the blood via the thoracic duct (Fig. 87), while others must first proceed to the liver by the portal vessels for further elaboration before entering the blood.

It will be remembered that the villi are found only in the small intestines; in the large intestines there are no villi. It must not, however, be supposed that absorption in the latter is exclusively carried on by the bloodvessels, for the large chain of glands, along the colon in particular, suggests as probable that in greater or smaller quantity the material absorbed passes through these glands, as through the glands of the mesentery, before entering the circulation. There is, at any rate, a well-developed lymphatic system in the walls of the large intestine, and it is certain that material is taken up from this bowel both by the bloodvessels and the lymphatics. The amount of this must be considerable, in view of the size of these bowels and the character of their contents.

Substances can be taken up with extreme rapidity from the large bowels. Colin observed that eighteen minutes after injecting a solution of nux vomica into the cæcum of the horse convulsions began, and eight minutes later the animal was dead. Anæsthetics, such as ether, may also be administered per rectum and produce narcosis. Finally, and from some points of view most important of all, proteins may be absorbed from the rectum and single colon, in spite of the fact that there is no proteolytic ferment to render them soluble.

Absorption of Fat.—If a cannula be placed in the thoracic duct of a starving dog, the lymph which escapes is identical with that from any other part of the body. If the animal be now fed on a diet rich in fat, the lymph becomes milky, and even the blood-plasma becomes turbid from fat, if the contents of the duct are permitted to enter the general circulation. It is evident that the lymphatics are the chief path by which the fat enters the body, for comparative analysis of the blood of the portal vein and carotid artery shows that the amount of fat in the two is the same. Nevertheless, the bloodvessels are not without some action in the matter, as will presently be shown.

It has been stated (p. 264) that fat in the small intestine is both saponified and emulsified, the former being a chemical, the latter a physical change. These processes result from the separate and combined actions of the pancreatic juice and bile, and they give rise to two possible views of the mechanism of fat absorption. Emulsification reduces the fat (and fatty acids) to a state of subdivision into particles so minute that they might conceivably be simply passed as such, through the epithelial cells of the villi to the lacteals, by an activity of these cells comparable to the ingestive powers of a white blood-corpuscle. This would readily account for the characteristic appearance of chyle

(p. 286), the minuteness of the fat particles it contains being probably intended to prevent embolism from plugging of the capillaries. The view here indicated was the one formerly most prevalent. On the other hand, bile has, in virtue of its bile salts, an extremely active solvent action on both fatty acids and soaps; hence the possibility that fat is split up so as to give rise to variable relative amounts of substances, which pass *in solution* into the cells of the villi, as do the proteins and carbohydrates. We shall see that the chemical view is the one now generally adopted.

If the intestinal mucous membrane of an animal in full fat absorption is stained with osmic acid, the epithelial cells are found to be crowded with minute particles of varying size, whose blackness shows them to be fat (Fig. 88). This fact provided the chief support for the view that fat reaches the lacteals in a state of minute mechanical subdivision not necessarily involving much chemical change. If this were so we should expect to see some of the fat particles in transit through the striated border of the epithelial cells, and this is never observed.

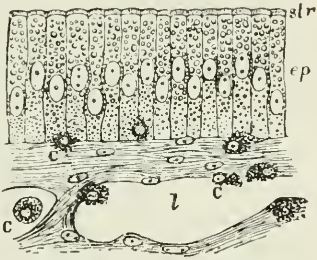

Fig. 88.—Mucous Membrane of Frog's Intestine during Absorption of Fat (Schäfer).

ep, Epithelial cells; *str*, striated border; *c*, lymph corpuscles; *l*, lacteal.

It is generally accepted that the fat passes into the cell and not between the cells, and the question arises as to whether this passage into the wall of the bowel is a physical or a secretive process. Leucocytes are not credited with absorption, though as carriers of fat between the epithelial cells and the central lacteal—viz., through the arterial network of the villus—they may assist. On the other hand, the absorption of anthrax bacilli from the intestine, a process which is undoubted, must occur from their being engulfed by cells. The wandering cells of the body are, we know, capable of ingesting bacteria in other places, and there appears no reason why they should not be so in the intestines. Nevertheless, there are good reasons for believing that the fat is dissolved and absorbed by the epithelium of the intestine, its solution into fatty acids and glycerol having been effected by the combined action of the bile salts and pancreatic lipase. These split products are readily absorbed, glycerin presenting no difficulties, while the fatty acids are taken up either as such or as soaps. It has been stated that osmic acid staining reveals the fact that fat as such exists in the epithelial cells. It is evident from this that the fats after solution are reconstructed into neutral fats within the epithelial cells. The synthesis of fats in the intestinal epithelium is effected by the same ferment, lipase, which originally split it up; it is not difficult to imagine a reverse action of lipase bringing this about. If an animal be fed on fatty acids without glycerol, neutral fats are found in the thoracic duct. Somewhere, therefore, the fatty acids have picked up glycerol, and this is believed to be in the intestinal wall, lipase effecting the reconstruction. The story is interesting and instructive; it emphasises the specific and selective influence of the living cell, regarding which further evidence will be given later. In the above process the valuable action of the bile salts in dissolving the fatty acids, and so assisting the lipase of the pancreatic secretion, is very evident.

When an animal is receiving a known quantity of fat in the food, and the whole of the chyle from the thoracic duct is collected with the object of recovering it, a portion of the fat is found to be missing. In these circumstances only 60 per cent. of the fat can be recovered from the chyle, and that which is missing is believed to be absorbed by the bloodvessels of the villi as fatty acids and soaps, and taken to the liver before its entry into the general blood-stream. This theory receives further support from the fact that after ligature of the thoracic and right lymphatic duct, 30 to 40 per cent. of fat is absorbed from the intestine. Even after excision of the pancreas, fat absorption is not entirely abolished, and, strange to say, more may be found in the intestinal canal than was given by the mouth. This suggests that fat may even be excreted by the intestinal wall.

All fats are not equally absorbed. In the dog olive oil is taken up more completely (97 per cent.) than any other fat; next comes mutton fat, of which 90 to 92 per cent. is absorbed; while of spermaceti only 15 per cent. is taken up. A dog may absorb up to 21 per cent. of fat in three or four hours, double that in seven hours, and 86 per cent. in eighteen hours. Absorption of fat, in ruminants especially, is a most important question, considering the large sums spent in adding fat to the diet of animals intended for food. Experimental inquiry shows that 90 per cent. of the fat in linseed cake, 79 per cent. in rape cake, and 88 per cent. in decorticated cotton cake can be absorbed. The digestive power of the horse for fat is lower than that of ruminants; only 53 per cent. of the fat in linseed cake can be utilised by this animal.

The following table shows the power possessed by the herbivora of digesting fat from different food substances, and demonstrates the relatively weak powers of the horse in this respect:

	Horse.	Ruminant.
	Per Cent.	Per Cent.
Grass - - - -	20	66
Hay - - - - -	24	50
Oats - - - - -	70	83
Barley - - - -	42	89
Maize - - - -	61	85
Beans - - - -	13	86

All the above foods in the matter of fat, and we shall see presently in the matter of carbohydrates and protein, are richer and more nourishing for the ruminant than the equine, owing to the different powers of absorption in the two classes.

Food Absorption.—At this point it is necessary to digress somewhat, and to glance at the question of the absorption of the various proximate principles of food—viz., protein, fat, and carbohydrate.

The economic feeding of animals has led to the chemistry of food absorption being inquired into by series of laborious experiments which have been carried on for years. Each class of animal has a different power of utilising the same food; for example, grass and hay are more nourishing to the ox and the sheep than to the horse, and the ox can utilise more than the sheep.

If a food were entirely digested and absorbed, there would be no fæces excepting the waste liquid secretion of the digestive tract. There is, of course, no ordinary food substance capable of complete absorption; there are indigestible substances which cannot be dealt with and are excreted; and in the herbivora the quantity of these must necessarily be very large. But entirely apart from indigestible matter, there is only a proportion of each of the proximate principles of a food which can be absorbed. The protein, fat, carbohydrate, and cellulose of every food substance have a distinct rate of absorption in each class of animal. Taking hay as an example, the horse can, as a mean, digest:

	Per Cent.
Protein - - - - -	57
Fat - - - - - -	24
Carbohydrates - - - -	55
Cellulose - - - - -	36

There is no way of causing a larger percentage to be absorbed, and so of rendering a given amount of hay more efficient. Absorption of the food principles is unaffected by rest or work. The horse absorbs no more per cent. if the diet is increased; he can extract no more per cent. if the amount be reduced. Feeding experiments show that around 57 per cent. protein and 55 per cent. carbohydrates lies the digestive capacity of the horse for these promixate principles in hay.

If we take the figures for the ox and the sheep, for the purpose of comparison, we get the following table:

	Ox.	Sheep.
	Per Cent.	Per Cent.
Protein	57	57
Fat	49	51
Carbohydrate	62	62
Cellulose	58	56

These facts are of extraordinary importance in the feeding of animals. The practical conclusions to be drawn from them belong to the realm of hygiene. They are mentioned here owing to their physiological aspect, for though we cannot explain the reason, there is no doubt that both ox and sheep in the matter of food absorption are physiologically superior to the horse, while no animal approaches the pig in the thoroughness with which absorption and consequent utilisation of food substances occurs.

Absorption of Carbohydrates.—We have seen (p. 264) the digestive changes undergone by starch in order to prepare it for absorption, and we have learned that in the body only the monosaccharides, such as dextrose, levulose, and galactose, but especially dextrose, are capable of being utilised, while the di-saccharides—lactose, cane sugar, and maltose—have all to be reconstructed in order to fit them for absorption. The following brief summary shows by what means the carbohydrates are prepared for entry into the body:

Starches are converted by means of the saliva and the *amylase* of pancreatic juice into maltose and dextrin, and then inverted by the ferment *maltase* into dextrose.

Lactose requires inversion by *lactase* into dextrose and galactose.

Cane sugar requires inversion by *invertase* into dextrose and levulose.

If an attempt be made to cause the organism to use up such sugars as cane sugar without passing it through the inverting process, as, for example, by injecting it subcutaneously, it is excreted unchanged in the urine.

If very large amounts of cane sugar, or even of dextrose, be given, they are taken up unaltered, probably by the lacteal vessels, and excreted by the kidneys. This constitutes the temporary glycosuria which sometimes follows a diet rich in carbohydrate. The lacteal path of absorption of sugars is of interest, for, as we shall see presently, physiologists have assigned the bloodvessels as the path by which sugar is taken up. Nevertheless, years ago Colin insisted that in the herbivora the chyle vessels took up sugar. The chyle of a horse on an ordinary diet of hay and oats was found by him to yield 13 to 16 per cent. sugar, and several such observations are referred to by him in terms which lead one to believe his experiments were adversely criticised by Bernard. The physiologist of the present day regards the bloodvessels of the villus as the path by which the sugar mainly gains entrance to the body. From here it is carried to the portal vein, and passes direct to the liver. We have seen (p. 253) that the sugar percentage in the portal vessel may vary: 0·4 per cent. has been found after a heavy carbohydrate meal in the dog, and 0·2 per cent. in the same animal during starvation. On the other hand, a definite percentage is maintained in the other vessels of the body, and the cause of this has been fully considered elsewhere (pp. 256, 269).

The absorption of carbohydrate by the animals of the farm has been the subject of considerable investigation. The ruminant in all cases is better in this respect than the horse, as may be seen from the following table:

	Horse.	Ox and Sheep.
	Per Cent.	Per Cent.
Hay - - - -	24	50
Clover hay - - -	29	53
Oats - - - - -	70	83
Barley - - - -	42	89
Maize - - - -	61	85
Beans - - - -	13	86

The practical application of these facts is very evident. All the above foods in a given quantity are richer for the ruminant than for the horse. In dieting horses, according to the market value of grains, it is well to ascertain what proportion of the proximate principles of the grain chosen are digested, or it may prove far from economical.

Absorption of Proteins.—Proteins, we have seen, are incapable of absorption as such. *Pepsin*, *trypsin*, and *erepsin* convert them into peptones and proteoses, and in this form, or when still further broken down by *trypsin* and *erepsin* into amino-bodies, they are taken up by the bloodvessels of the intestine. It is not known what extent of hydrolytic action is necessary before absorption can occur; certainly it must be carried as far as production of proteoses and peptones. If the thoracic duct of a dog be ligatured, and a large protein meal given, it is perfectly absorbed, as shown by the increase in urea. Clearly, therefore, the path of absorption for protein is the bloodvessels, the material passing by the portal vein to the liver. From this it might be supposed that proteose and peptone may readily be found in the general circulation, but, as a matter of fact, there is no blood in the body, including that of the portal area, which contains even a trace of peptone or proteose; in fact, these substances in the circulating blood are poisons, give rise to peptonuria, and are excreted by the kidneys.

Some proteose and peptone in their passage through the epithelial cells of the intestinal wall may be resynthesised. How and in what way this is brought about is unknown. We saw that the same thing occurred to the fats before they could pass into the lacteals. Proteins administered by any other channel than the digestive canal are excreted—egg-albumin, for instance, if injected into the blood—and got rid of by the kidneys. Foreign proteins are of no use until they have passed through the proper laboratory—viz., the intestinal canal—and that something more than splitting the complex protein molecule occurs is evident from the fact that some rearrangement of the molecule occurs which enables it now to be built into and form part of the protein tissues of the living body.

The absorption of protein by animals is an important question in feeding. We saw that, in capacity for absorbing fat and carbohydrate, the horse was distinctly inferior to ruminants. In the matter of protein absorption the horse is sometimes superior to the ruminant, and in all cases will bear comparison with it, as may be seen from the following table:

	Horse.	Ruminant.
	Per Cent.	Per Cent.
Fresh grass - - -	59	70
Hay - - - - -	57	57
Wheat straw - - -	19	17
Oats - - - - -	79	79
Barley - - - -	80	70
Maize - - - -	77	74
Beans - - - -	86	88

Absorption of Water and Salts.—By means of the bloodvessels water is readily absorbed, though all parts of the digestive tract are not equally active in this respect. There is probably no absorption of water from the stomach of any animal. There is very little absorption of this fluid from the small intestines, whereas in all animals the large intestines are the chief seats of its absorption. In the horse the cæcum, in other animals the large colon, is the chief seat.

In the matter of the absorption of salts, a good object-lesson of the peculiar selective powers of the epithelial cells is obtained. Chlorides are readily taken up, but sulphates only with difficulty; iron is taken up, but its near ally, manganese, is absorbed with difficulty. Though these facts suggest that the process is one of secretion rather than of physical action, yet it is impossible to neglect physical factors as playing a part. Finally, Colin's experiments on herbivora showed that absorption of salts, such as prussiate of potash, iodide of potassium, tartar emetic and many other substances, and of colouring matters such as chlorophyll, occurred through the chyle vessels, though not necessarily exclusively.

Much of the foregoing refers to absorption from the small intestine, but it would be wrong if we failed to emphasise the fact that in the herbivora especially, the large intestine is the seat of vitally important digestive processes. An attempt has been made (p. 227) to describe these in the light of our limited knowledge, but the picture is a very imperfect one. The question is only referred to here in order to emphasise the fact that the large intestines, though they have no villi and no secretion other than the succus entericus, are important seats of digestion and absorption. A man may manage to get along without his large intestines; the horse could manage with half his present length of small intestine but he could not afford to spare an inch from his large bowels. So imperfect is our knowledge, because of the difficulties attached to experimental inquiry in the larger animals, that we do not know the absorptive function of any portion of the large intestine; we know only the bare fact that it does absorb. At p. 226 attention is drawn to the remarkable fact that a few inches in the intestines of the horse separate fluid fæces from solid fæces. Who can doubt the important changes which must be taking place in those few inches? In their anatomical arrangement the ox and the sheep are very similar—almost identical, in fact. Their diet is identical, perhaps their digestive processes are identical, up to a certain point; then they differ widely: the fæces of the sheep are firm and dry, those of the ox soft and unformed. There must be important differences in the intestinal absorption of animals which bear such close resemblance to each other.

Several matters referred to in this chapter will have to be dealt with in greater detail in the chapter on Nutrition.

CHAPTER VIII

THE ENDOCRINE GLANDS AND INTERNAL SECRETIONS

THE *endocrine*, originally known as the *ductless glands*, are represented by the spleen, thyroids, thymus, adrenals, the pituitary and pineal bodies. Until recent years the function of these was entirely unknown, and those of small size, such as the adrenals, pituitary, and pineal, were regarded as too insignificant to merit attention. It is now known that these glands command sometimes the life, and at all times the well-being, of the individual, and that their removal in some cases means certain death. Their function is to produce an *internal secretion*, a chemical substance, or *hormone*, which is poured into the blood and utilised elsewhere in the body. Ductless glands are not the only bodies producing an internal secretion; the liver, pancreas, testicles, ovaries, and prostate produce, in addition to the evident secretion, a substance or substances which find their way into the circulation by the lymph or bloodvessels. The chemical nature of the internal secretions is imperfectly known; they are protein in character, and are not destroyed by boiling, a characteristic which distinguishes them from ferments. *Infundibulin* may be selected as an example; its active substance is soluble in water, dialysable, insoluble in alcohol or ether, and unaffected by repeated boiling, drying, or sterilisation.

All the light which recent inquiry has thrown on the function of the endocrine glands arises from the epoch-making discovery of *secretin* (p. 260) by Starling and Bayliss.

The Spleen.—This is the largest ductless gland in the body. It possesses neither an internal nor external secretion, and in spite of the numerous observations to which it has been subjected, is still a physiological enigma. Its vascular arrangement is peculiar in that it is capable of holding a considerable quantity of blood, and for this purpose readily lends itself to change of size. Further, it is the only tissue in the body where the cell elements are directly bathed in blood without the intervention of even a capillary wall. The spleen contains a considerable amount of involuntary muscular fibre, and is capable of movement. These movements have been carefully studied, and it is established that they are of two kinds. One is a slow expansion due to unknown causes, which occurs after a meal; it reaches its maximum about the fifth hour, and is followed by contraction. The other is a rhythmical expansion and contraction occurring in certain animals, such as dogs and cats, at intervals of about one minute. It is believed that the latter movement is for the purpose of assisting the circulation through the organ, to which the splenic pulp offers considerable resistance. That the movement is brought about by the bands of involuntary muscular fibre is undoubted; the spleen is liberally supplied with motor nerves carried in the splanchnic, and stimulation of these leads to a reduction in the volume of the organ. It is also considered that there are nerves to the spleen, which on stimulation produce dilatation.

The *use of the gland* is largely based on conjecture. By some it has been considered the seat of formation of red blood-corpuscles, and that this is the case during intra-uterine life and shortly after birth is undoubted; but there is no evidence of this function in the adult. It has been claimed to be the seat of destruction of the red cells and of phagocytosis, and as bases for this theory there are some telling facts; for instance, certain large amœboid cells found in the spleen are capable of ingesting and destroying worn-out blood-cells and other solid matter such as micro-organisms, while the richness of the splenic pulp in iron is regarded as due either to the hæmoglobin of the destroyed red blood-cells being stored up for future use, or to the preparation of new hæmoglobin. That the conservation of iron is one of the functions of the spleen would appear from the fact that removal of this organ in dogs causes a distinct daily loss of iron. The theory is very plausible, though by no means definitely proved; at the same time there is great difficulty in rejecting the view that filtration is a function, since the spleen appears in every way to be admirably suited to act the part of a blood-filter.

The lymphoid tissue of the spleen, like lymphoid tissues in general, is capable of forming a substance from which uric acid may be readily produced, and the spleen has in consequence been regarded by many as the seat of active metabolic changes with the formation of uric acid. The evidence, however, is not sufficiently conclusive to warrant uric acid being regarded as a special product of the spleen.

Some physiologists have suggested that the spleen produces an enzyme which converts trypsinogen into trypsin. There is no reason why the spleen might not do so, but it by no means follows that this is normally its function, nor would there appear to be any necessity for this action, as this conversion is one of the special duties of the intestinal juice.

In connection with all these theories it is well to remember that the spleen may be removed completely, and no ill effects follow.

The Thyroid and Parathyroid Glands.—The relationship between the thyroid gland and disease was first established in connection with *goitre*, and, later, with a pathological condition known as *Graves' disease*. In both of these affections the glands are enlarged, and surgical attempts to remedy goitre led to the production of another affection known as *myxœdema*. It was evident, therefore, that either excessive secretion or defective secretion by the thyroids was capable of producing serious pathological conditions, and when these facts had been established by clinical experience, experimental inquiry on the thyroids of animals was undertaken.

This work led to very contradictory information being obtained; when thyroidectomy was practised on the carnivora the majority of the animals died, while of the herbivora so operated upon one-half recovered. It was soon found that the thyroid consists of two distinct portions, one part the thyroid proper, the other the parathyroids, of which there are one or two to each gland, depending on the species of animal. The symptoms following removal of the thyroid were ascertained to depend upon whether the thyroid, parathyroids, or both, were included in the surgical procedure. The disturbances produced by removal, partial or complete, of the parathyroids are essentially distinct from those characteristic of thyroidectomy. In the former case the most striking disturbances are nervous in type, and consist of clonic or tonic muscular contractions, followed by convulsive movements, the so-called 'tetany' of parathyroidectomy; in the latter the disturbances mainly affect general bodily metabolism, occasioning that depression of tissue activity as a whole so well exemplified in the lowered bodily and mental vitality characteristic of the cretinous, goitrous, and myxœdematous states. If all parathyroids be removed death usually results within a few weeks, the symptoms being most acute in carnivora and in the young of herbivora. Young animals are more affected by thyroidectomy than fully grown ones, as has been clearly shown by Sutherland Simpson's experiments on sheep and lambs. The convulsions attending removal of the parathyroids are said to be abolished by injections of extracts of the gland; while the injection of calcium salts effects a cure of all the symptoms produced by removal of these bodies.

A jelly-like colloid substance constitutes the internal secretion of the thyroid, which is the only endocrine gland which can store its secretion, but forms no part of the secretion of the parathyroids. Histologically the thyroid gland consists of vesicles lined by a single layer of cubical epithelium, while the parathyroid is composed of irregularly arranged columns of epithelium-like cells. The gland contains a nucleo-protein in addition to a colloid substance; the latter is not a nucleo-protein, and is remarkable for containing iodine in organic combination with protein. The iodine-containing substance, abundant in herbivora, is termed *iodothyrin;* it is a brown amorphous material, containing phosphorus and 10 per cent. of iodine.* The parathyroids contain no iodine.

The internal secretions of the thyroid and parathyroids are not identical in function. That of the parathyroids depresses the excitability of nerve cells, so that, when these minute bodies are removed, the nervous symptoms, described above as tetany, result. The thyroid secretion is not identical in function with that described above. It lowers blood-pressure, leads to the rapid excretion of lime salts, and is largely concerned in the metabolism of the body. The removal of the glands is followed by a reduction in the nitrogenous and fat metabolism, and permits abnormal amounts of carbohydrates to be consumed without glycosuria resulting. In the young subject a diminution or absence of thyroid secretion prevents the physical and mental development. The genital glands are undeveloped, and the adult remains a child, as is witnessed in *Cretins*.

White rats fed upon fresh ox thyroid suffer from hypertrophy of the adrenals, kidneys, pancreas, and heart, as the result of greatly increased metabolism; if the feeding be continued it causes death. There is also in young animals inhibition of the growth of the uterus and of the pituitary body. It will be observed that the adrenals are enlarged, while the pituitary is diminished in size. This is evidence of the correlation which exists between the various internal secretions, and to which attention will later be directed.

The Thymus.—This body, composed of modified lymphoid tissue, is of use mainly in fœtal and very early life; later on it atrophies. Nothing is known of its function, though it is observed that castration appears to have an effect on its disappearance. The process of atrophy is much slower in the castrated as compared with that in the uncastrated animal, while its early absorption or experimental removal has been observed to be associated with a rapid growth of the testicles.

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* Kendall has recently isolated a pure crystalline substance, an indole compound of perfectly constant composition, called *alpha-iodine*. It contains over 60 per cent. iodine.

The Adrenals.—The adrenals consist of two distinct tissues, a medulla, which can be shown to be derived during the process of development from the sympathetic nervous system, while the cortex is formed from the mesoblast. While very little is known of the function of the cortex, the medulla is essential to life, and yields under experimental inquiry some remarkable and characteristic results.

The experimental removal of the adrenals in any animal is rapidly followed by death preceded by symptoms of great muscular prostration and diminution of vascular tone. In Addison's disease in man these bodies are affected, and give rise to much the same symptoms as above, and in addition bronzing of the skin is present.

An extract of the medulla of the gland, when injected into the blood, after section of the vagi, increases both the rate of rhythm and the tone of the cardiac muscle, and causes a contraction of the bloodvessels, which produces a remarkable increase in blood-pressure.* This increase is of a purely temporary nature, which indicates that the active principle is destroyed in the circulation. Within a few minutes the heart-beats return to the normal and the blood-pressure falls. When the vagi are intact, injections give rise to a slowing of the heart and frequently to stoppage of the auricular beats. The active principle known as *adrenalin* can be detected in the veins leaving the gland, so that there can be no doubt that it is poured into the blood, where it regulates the rhythm and tone of the heart muscle and maintains blood-pressure. In this important function the adrenals are probably assisted by another internal secretion, to be considered presently—namely, that from the pituitary body.

The action of adrenalin in causing constriction of the bloodvessels is turned to account in minor surgery in controlling hæmorrhage.

It is believed that the adrenals possess secretory nerve-fibres derived from the splanchnic, and that stimulation of these increases the amount poured into the vein of the gland. Adrenalin acts upon all plain muscle and gland-cells which receive sympathetic fibres, and it is distinctly noteworthy that the effects are identical with those produced by stimulation of the sympathetic fibres (Langley), of which system the medulla of the gland is, as pointed out above, merely an outgrowth.

It is probable that the function of the medulla of this gland is concerned in the provision of a substance intimately connected with muscular metabolism, and more particularly with 'tone,' possibly of the skeletal muscles, but especially of the muscular fibres of the circulatory system. Adrenalin causes an increased conversion of glycogen into sugar. There is considered to be some connection between the cortex of the adrenals and the sexual system. During the breeding season in some animals the glands enlarge, and in rabbits the cortex of the gland becomes twice the normal thickness during pregnancy. It is believed that in man a connection exists between the adrenals and the growth of the body, development of puberty, and sexual maturity.

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* Oliver, and Sharpey-Schäfer.

Under the influence of emotion, great muscular effort, fright, or anger, the medulla of the adrenals pours out an excessive secretion as the result of impulses received from the brain through the sympathetic system. This secretion may be regarded in the light of a defensive mechanism against the nervous explosion; the muscles are 'tuned up' for an extra effort, an increased quantity of glycogen is rendered available for their use, the general blood-pressure is raised, and the thyroid co-operates by furnishing a substance intended to restore the exhausted nerve cells. Whether the storm results in fight, as is common in the case of dogs, or flight, as in the case of horses, probably depends almost entirely on the testicular secretion. In the absence of these glands, it is easy to understand the gelt animal taking no risks, and deciding to get away as early as possible from the source of danger. The female in the defence of her progeny will put up a fight under the influence of the internal secretion of the ovary; and this applies to all animals from the elephant to the barn-door fowl.

The Pituitary Body.—This gland consists of three portions, an anterior lobe derived from the buccal ectoderm, a posterior or nervous lobe separated from the anterior by a cleft, while the nervous lobe is separated from the cleft itself by a narrow strip of tissue, consisting of modified glandular tissue, known as the intermediate portion.* This part is formed by the neck or stalk of the pituitary. The nervous lobe is composed of neuroglia cells, and is remarkable in the ox for its vascularity. Bell† emphasises the importance of regarding the pituitary as one organ, and not two.

The internal secretion of the pituitary has been known as *Pituitarin*, but Bell has shown that the active substance is prepared only from the posterior lobe, and it is accordingly called by him *Infundibulin*. The effect of this on injection into the body resembles that of adrenalin in its actions on the heart, bloodvessels, and skeletal muscles. It causes the blood-pressure to rise, and increases the tone of the heart muscle. Though it constricts the arterioles generally, it causes dilatation of those of the kidney, accompanied by diuresis.* This diuresis, however, may be due to a specific action on the cells of the kidney. Infundibulin may also slow the heart. The action of infundibulin on smooth muscle differs from that of adrenalin by not occurring through the sympathetic system, and further, contrary to what would happen in the use of adrenalin, the pressor effects are not obtained by a second injection within a short period of time. An extract of the posterior lobe excites contraction of the intestinal wall, and of the œstrus and pregnant uterus, but not of the resting organ (Bell). Further, it possesses a substance containing glycogenlytic properties, and one which acts as a galactagogue on the secreting mammary gland. There is, however, good reason for believing that the increased flow of milk is due to contraction of the smooth muscle of the mammary alveoli. Bell points out that one of the normal functions of the pituitary is to retain the alkaline bases in the tissues; in this respect, and in its effect on blood-pressure it is antagonistic to thyroid secretion.

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* Herring.

† 'The Pituitary,' W. Blair Bell, 1919.

Experimentally it has been proved by Bell that compression of the infundibular stalk in the dog leads to atrophy of the genital organs, uterus, ovaries, and mammæ, together with immense deposits of fat. The animal remains lethargic, and spends most of its time in sleep, from which it has to be aroused for food. Removal of the anterior lobe causes degenerative changes in the ovaries, but no such result follows removal of the posterior lobe. Removal of the entire body causes death.

In hibernating animals the pituitary undergoes very marked changes during hibernation, and the large deposits of fat then to be seen may be due to insufficiency of this gland. Enlargements of the pituitary glands are associated with a singular disease in the human subject—*acromegaly*—characterised by an overgrowth of the bones of the face and extremities, resulting in gigantism.

The Pineal Body remains a physiological enigma, though it is believed to be concerned in the production of sexual maturity.

In forming a clear concept of the function of the endocrine glands it is all-important to regard them collectively and not individually. Everything points to an inter-relation of functions; these may be mutually stimulating or mutually restraining. For example, *infundibulin* counteracts the low blood-pressure occasioned by thyroid secretion and the rapid excretion of lime salts produced by this gland. Eagerness to fight is decided by the brain, but under the stimulus of the testicular secretion; and simultaneously the pituitary and adrenals raise the blood-pressure, while the voluntary muscles are furnished with an extra supply of fighting material in the form of glycogen; then the thyroid co-operates by restoring nervous energy and lowering the blood-pressure after the storm.

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* Sharpey-Schäfer.

The extraordinary importance of the endocrine glands to the genital system cannot fail to have been observed. Periodical sexual excitement in both male and female; the growth and development of the sexual organs; the sympathy between the uterus and mammary glands; the fertilisation and implantation of the ovum through the internal secretion of the corpus luteum; the growth of the mammary gland through the production by the fœtus of a hormone, which finds its way into the maternal blood; the alteration in the eating qualities of the flesh of castrated animals; the modification of sex characteristics, especially in the male, resulting from this operation; the absence of antlers and in some animals (sheep) of horns in consequence of castration; the persistence of lactation after ovariotomy (cow); the influence of the testicles and ovaries on psychical conditions, even the storage of fat in the body, are all examples of the point under consideration. Nor, as we have seen, are internal secretions confined to ductless glands. The liver, with its external secretion of bile, has an internal secretion of glycogen and urea; the pancreas, with its obvious secretion of pancreatic juice, has an internal secretion which regulates the destruction of sugar; and the kidney has been described as also possessing an internal secretion. It is believed by some that *secretin* is responsible not only for the production of pancreatic juice, but also of the bile and succus entericus; that gastric juice is the outcome of a hormone, *gastrin*, secreted by the pyloric wall; and that intestinal peristalsis may even be activated by a hormone furnished by the appendix of the cæcum.

Only the beginning of a study of the endocrine glands has at present been made; the future of this branch of physiology may hold in its keeping some of the romances of science. Keith* has recently propounded the theory that the differentiation of mankind into racial types is a function of the endocrine glands. He suggests that the pituitary regulates growth, cast of feature, texture of skin, and character of hair; that the internal secretion of the testicles determines the robust manifestations of the male, which are not identical in Caucasian, Mongol, and Negro; that the adrenals are probably concerned in race pigmentation, and the thyroid in implanting racial characteristics.

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* British Association for the Advancement of Science, 1919.

CHAPTER IX

THE SKIN

It is obvious that one important function the skin discharges is that of affording cover to the delicate parts beneath; where-ever the chance of injury is greatest, the skin is thickest, while in those parts where sensibility is most required it is thinnest. The skin of the back, quarters, and limbs affords a good illustration of the first kind; on the back a protective covering is found which, in some horses, is as much as $\frac{1}{4}$ inch in thickness. The skin of the face and muzzle is a good example of the latter variety, the skin in some parts being as thin as paper. In those regions not exposed to violence it is also thin, as on the inside of the arms and thighs. In spite of the thinness of the skin its strength is remarkable; a horse's body may be dragged along by the thin skin of the head.

The skin as an organ of touch is of great importance. All animals appear most sensitive to even slight skin irritation; flies will cause horses considerable suffering, and the elephant, despite its thick hide, is quite as intolerant of these tormentors as is a well-bred horse. The skin is highly endowed with sensory nerves, especially that part connected with the organs of prehension; the long hairs, 'feelers,' growing from the muzzle of the horse end in special tactile structures in the skin (Fig. 89).

The skin is a bad conductor of heat, and in this retention of heat is considerably assisted by the layers of fat found beneath or at no great distance from it, as in the abdominal region; it is the subperitoneal fat which protects the viscera of animals living in the open and lying in wet places. The epidermal covering of the skin relieves the parts beneath from excessive sensitiveness; through the sebaceous secretion it assists in preventing loss of heat, while the greasy covering thus produced helps the hair to throw off rain, prevents the penetration of water, and so saves the epidermis from disintegration. Horn is skin which has undergone a modification.

Hair.—Not all parts of the body are covered by hair. There is very little on the muzzle and lips, and it is very scanty on the inside of the thighs, inside the cartilage of the ears, and on the mammary gland and genitals. By means of the hair the heat of the body is maintained and prevented from passing off too rapidly. The thickness of the hairy covering varies considerably with the class of horse; the better bred the animal the finer the coat. Draught horses yield between 3¼ to 3½ kilogrammes (7 or 8 pounds) of mixed hair, dirt and dandruff by clipping; in a well-bred horse this would be reduced to 283 grammes (10 ounces), or even less; the amount of hair of the mane and tail is about ¾ kilogramme 1½ pounds).

It is a well-known fact that the hair of every part of the body, excepting that of the mane and tail, has only a temporary existence, and is changed twice a year, once for a thick, and once for a fine coat. During this period horses are generally regarded as not being at their best, and changing the coat is always urged as a cause of loss of condition or stamina. The permanent hair is not entirely represented by that of the mane and tail; the eyelashes and the fetlock hair are permanent, also the long tactile hairs on the muzzle. The temporary hairs on the horse are of two kinds, which can be distinguished only by their rate of growth. If a part be clipped, or, preferably, shaved, and the growth watched, in a short time it will receive a scanty covering of long, rapidly growing hair, followed by a slow growth of ordinary hair. There is no difference in the two hairs, excepting the length. The long, rapidly growing hairs are known as 'cat hairs'; they are not numerous, being about 4 per square centimetre (27 to the square inch), while the ordinary hairs are nearly 700 per square centimetre (4,300 to the square inch). It may yet be shown that 'cat hairs' are tactile in function.

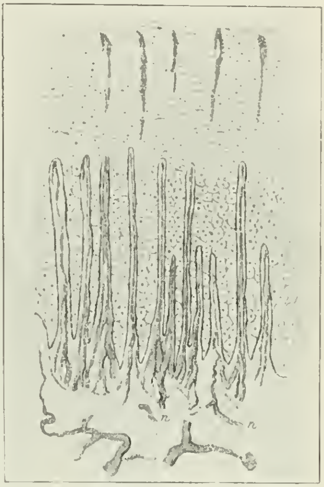

Fig. 89.—Section of Skin of the Horse's Lip, showing the Nerve Endings in the Touch Papillæ.

The growth of the hair is regulated by the surrounding temperature. If horses in the depth of winter are placed in a heated atmosphere, such as a horse deck on board ship, the majority commence to shed the winter coat in a few days, though the temperature of the outside air may be at freezing-point; similarly, if horses are taken from a warm to a cold locality, the hair responds by becoming longer. Speaking generally, the above statements are correct, but there are exceptions and modifications. Some horses do not shed the coat after passing into a warmer latitude; the mechanism which regulates the periodical shedding of hair refuses to respond to the changed condition of affairs, so that in passing from north to south of the Equator, with its reversal of seasons, the animal may grow a summer coat in winter and *vice versa* for at least a year after entering the new latitude.

The permanent hair of the body—viz., the mane and tail—may grow to almost any length, but the temporary hair of the surface of the body grows only to a definite length. The full length having been attained, nothing will make it grow longer, yet if the horse be clipped, hair at once grows rapidly, but only to its original length; in other words, everything required for the needful growth to occur is present, but there is a restraining influence which determines the length of hair according to the season.

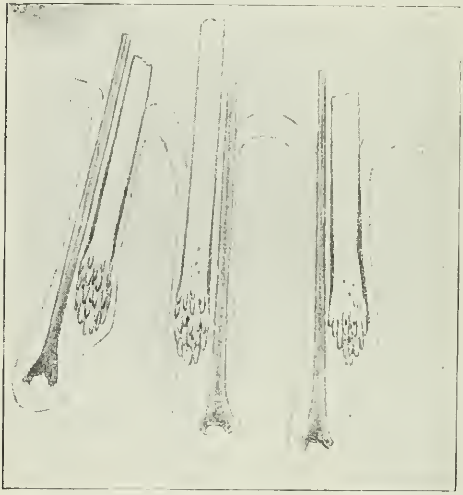

Fig. 90.—Section of Horse's Skin, showing the Casting Off of the Old Hair and Growth of the New.

It will be observed that both are emerging from the same follicle.

Hair Streams.—This term has been very aptly applied to the directions taken by the hair. Very little observation shows that, though the general trend of the stream is obliquely downwards and backwards on the neck and trunk, downwards on the face and limbs, and backwards on the cheeks, nevertheless, the stream alters its course in an interesting manner at various parts of the large surface, while whorls are frequent. The number and position of the latter are variable; indeed, it has been considered that no two horses are identically marked in this respect, and in Japan these whorls are employed for the identification of horses, much the same way as the finger-print system is employed for the identification of men. There are certain whorls seldom absent: one, the largest, may generally be seen in the flank; the hair over the loins distinctly divides as it approaches the crest of the ilium, one current passing over the quarters, another down the flank. This is met by a stream passing up the flank, which divides the hair right and left; on the left (if the near side be inspected) it passes forward and downwards over the flank, on the right it curves outwards to pass down the quarters. Another whorl may often be seen issuing from under the belly, just in front of the flank, and radiating upwards. The neck, below the angle of the jaw, has also a whorl, and there is one, occasionally more, on the forehead and face; there are many others not so regular, though frequently seen—for instance, on the poll, on either side of the neck, in the middle line of the neck, over the pectoral muscles, the stifles, and in diffuse areas below the knees and hocks. 'Feather' was the very apt term applied a century ago to the hair pattern of which we are speaking. In the present day feather is employed to designate the hair on the legs of cart horses.

The direction taken by the hair in animals and man has been made the subject of very critical study by Dr. A. Kidd,* who noted that the direction taken by the hair in primitive hairy mammals is simple and uniform, the slope being from head to tail, thus affording the least possible resistance to the passage of the animal through air, water, or brushwood.

There are three phenomena in the direction of the hair to which Kidd draws attention. These are *reversed areas*, such as may be seen on the arm of the dog due to resting on the part; *whorls*, *feathering*, and *crests*, which are so well seen in the horse in the convergence of hair streams; and, finally, *tufts*, seldom found in the horse, and, when existing, seen on the flank and over the extensor muscles of the hind limb. A 'tuft' resembles a stack of corn standing in a field.

Fig. 91 shows the frontal whorl of the horse; Fig. 92 the whorls, featherings, and crests on the pectoral region; and Fig. 93 the whorls, featherings, and crest on the side of the body. Kidd regards the phenomena of whorls, featherings, and crests as due to underlying muscular action, and produced by mechanical causes alone. He points to the primitive horse, zebra, and ass as being free from whorls, or in this respect only poorly developed, excepting for the universal frontal whorl, and he regards domestication with its concomitant work as the cause of the peculiar hair markings observed.

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* 'The Direction of Hair in Animals and Man,' 1903. Dr. Kidd has very kindly lent me his figures of the horse for reproduction.

The direction of the hair streams in cattle has been utilised as an indication of milk production. On the buttocks the hair grows in two different directions, upwards and downwards; at the line of junction a 'crest' is produced which extends to the udder, and in shape resembles a shield. The size of this shield-like area is stated by Guenon of France to bear a relationship to the milking properties of the cow. The larger the 'shield' the greater chance there is of the animal being a good milker. Guenon does not deny that a small 'shield' may be present in a good milker, but says that if the shield were larger she would be a better milker. The forms and shapes of the shield are

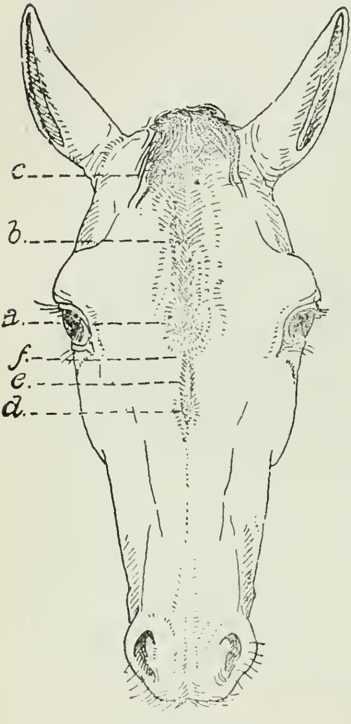


Fig. 91.—Frontal Region of the Horse (Kidd).

a, *b*, *c*, Universal whorl, feathering, and crest; *d*, *e*, *f*, occasional supplementing whorls, feathering, and crests.

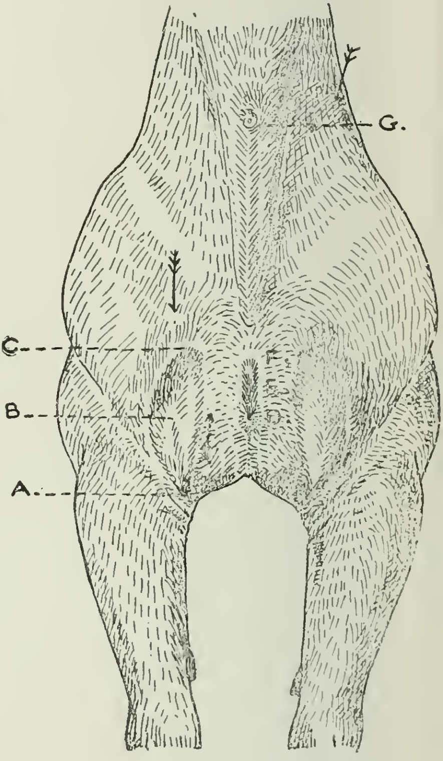
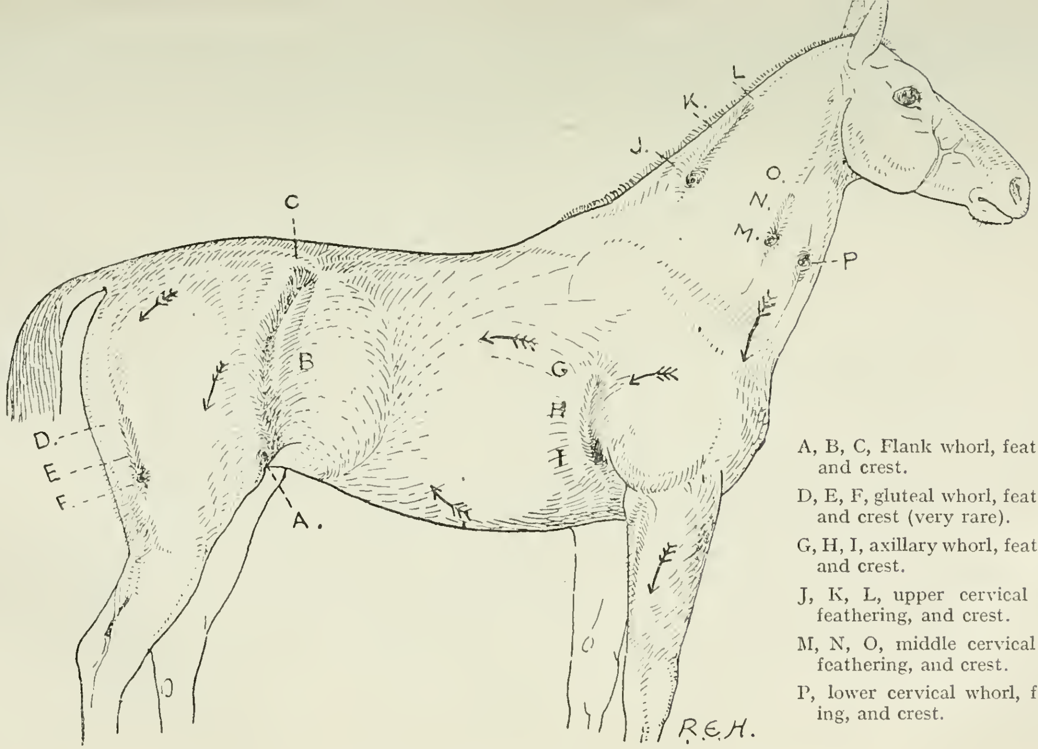


Fig. 92.—Breast, showing Hair Streams, Whorls, Featherings, and Crests (Kidd).

A, B, C, Universal pectoral whorl; D, E, F, rare central whorl; G, occasional whorl.

The arrows and lines denote the direction of the hair.



A, B, C, Flank whorl, feathering, and crest.

D, E, F, gluteal whorl, feathering, and crest (very rare).

G, H, I, axillary whorl, feathering, and crest.

J, K, L, upper cervical whorl, feathering, and crest.

M, N, O, middle cervical whorl, feathering, and crest.

P, lower cervical whorl, feathering, and crest.

Fig. 93.—Side View of Horse, showing Hair Streams, Whorls, Featherings, and Crests (Kidd).

The arrows and lines denote the direction of the hair.

various, and in this country no real importance has been attached to the sign.

Of the **pigment in hair** which gives colour to the coat, our knowledge, until quite recently, has been of the scantiest. The active investigation now being carried out of Mendel's theories of heredity made it essential in the special case of heredity in coat-colour to know more about the origin, nature, and behaviour of the hair pigments, and so we now have some information which is both interesting and promising.* Three different forms of 'melanin'—we use the name in its generic sense—are found in hairs—black, chocolate, and yellow. Of these, the black is extremely insoluble, and hence very difficult to deal with; so also is the chocolate pigment, though to a less extent. The yellow, on the other hand, dissolves readily in numerous solvents, and may thus be easily obtained. In its reactions it differs entirely from the black and chocolate pigments. In the case of mice there is now no doubt that their varying colours are due to the presence in their hairs of one or more of these three pigments. The less numerous experiments so far made with horsehairs suggest no doubt as to the different colours of horses being due to causes essentially the same as those which give the various colours to mice. As to the origin of these pigments, it has generally been presumed that they must be derivatives of hæmoglobin, but there are no pathological or purely chemical facts in definite support of this view. On the other hand, it has been shown† that an extract can be made from the skins of rats, rabbits, and guinea-pigs, which acts on tyrosine in such a way as to give rise to pigment substances. From the conditions under which the conversion is most readily effected, and the fact that the activity of the extract is at once destroyed by boiling, the active agent is regarded as a ferment, and, in accordance with the systematic nomenclature now used, is therefore known as *tyrosinase*. A further fact of extreme interest is that the colour of the pigment formed from tyrosine corresponds to the colour of the animal from whose skin the active extract is made. Black pigments are produced when animals are used whose skin contains black pigment, and yellow substances are obtained when the skin contains orange pigment.

Colours of Horses.—The body colour of animals is protective; whatever the tint may have been in the ancestors of horses it was intended to help in the struggle for existence. It is probable that the colour was dun. Far more protective colouring, however, is afforded another species of equine in the form of bars; the zebra under certain conditions of light is invisible. With the exception of black and greys, which are liable to turn grey or white, all other colours are practically permanent even to old age. We do know, however, that injuries to the skin of horses, even of a slight character, are commonly followed by a growth of perfectly white hair, which never regains its pigment. In these cases the skin also loses its pigment; pigment granules are not reproduced in injured skin. The connection between body colour and constitution is a physiological problem to which, unfortunately, no solution can be given. Colour and temperament may go hand in hand. Chestnut horses are frequently excitable, nervous, and irritable; all horses of light colour, no matter what it may be, are, as a rule, wanting in stamina and constitution. The 'mealy' bay is typical of a bad colour and almost invariably of a bad horse. Grey horses are not popular, and a race-horse is rarely of this colour, yet in the East such coloured horses are capable of great fatigue, and possess remarkable stamina, provided that the skin is pigmented. A grey horse with a pink skin is an albino, and is worthless for hard work. For work and hard constitution a roan is difficult to beat, especially a red roan, yet the colour is not popular. The 'softest' horse is the black, and on this point there appears to be no difference of opinion.

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* Florence M. Durham (Proc. Roy. Soc., vol. lxxiv., p. 310, 1904).

† *Loc. cit.*

It is seldom that the colour of a horse is not broken by the introduction of white; white is common on the face and limbs, and in days gone by a star on the forehead was so prized that one was created if it happened to be absent. On the limbs the amount of white is variable; no exception is taken to the white if limited, but four white legs are not only unsightly, but horses so marked are frequently wanting in stamina. White legs are liable to 'chap' in winter, for white on the limbs of a coloured horse is associated with a pink skin; such a skin is readily affected if washed and left wet.

Grey legs, contrary to white, are usually only found in grey horses, but grey horses may have grey legs or white legs. In horses of any colour white coronets mean colourless feet, and grey coronets black feet, for the reason that the skin of *grey* horses is pigmented. Black coronets are accompanied by a dark slate-coloured horn commonly referred to as black. A coronet with black-and-white markings gives a black-and-white striped foot corresponding to the position of the markings on the coronet. If the coronet is wholly white the hoof is without pigment; it is frequently spoken of as 'white,' but it is really yellow. White hair, provided it does not arise from age, grows only from a non-pigmented skin, and this condition constitutes albinism, so that white coronets and yellow feet indicate local albinism. Colourless feet are notoriously bad, and horses with white legs are, in consequence, generally disliked.

Face and Limb Markings.—Special attention has in recent years been drawn to the face and limb patterns produced by white hair in animals.* The face pattern may be symmetrical or one-sided, may cover the whole front and side of the face, and even involve the orbit. In this case the iris, sclerotic, and choroid partake of the non-pigmented condition, showing that this is not a mere accidental surface marking. Names have been given to face markings, but these need not concern us. Too much white on the face is a serious blemish, and a white muzzle with a pink skin is objectionable. In the paper referred to the writer stated that the amount of white on the legs will be in proportion to the amount of white on the face. If the 'star' is not in the middle line, he considered there would probably be a want of bilateral symmetry in the markings of the limbs. He also pointed out that the hind-legs are almost always more extensively marked than the fore-legs, and that it is very rare to see only white fore-legs. Hutchinson considered that, where there is want of symmetry in the markings, as, for example, the face-patch to one side, or two lateral legs white and their fellows coloured, it may be suspected that the animal is not developed with perfect bilateral symmetry in other respects. He may be a 'left-handed' horse, and, if so, even if strong and efficient, will move awkwardly and be unpleasant to ride. We do not share this latter view, but the whole matter is so interesting and the facts so readily collected, that attention is drawn to our ignorance of the question, and the necessity for observation.

Albinism.—This is the absence of pigment from the skin, and may be general or local. Local albinism commonly affects the face and legs. It may be extremely local, as in *wall-eyed* horses, who possess no pigment in the iris of one or both eyes. It may affect the whole surface of the body, as in *white* (cream-coloured) horses with a pink skin; or large areas of the bodies of such horses may be bay or black, and the remainder cream-coloured. In cream-coloured horses the choroid and iris are without pigment, the latter being bluish. A 'grey' horse is not a 'white' horse, though he may become white with age.

Clipping.—Experience shows that the heavy winter coat grown by horses is the cause of considerable sweating at work, and the general practice of clipping has therefore been introduced. Of its value there can be no doubt; it considerably reduces the risk of cold and of chest diseases, for animals on coming in from work may be readily dried and thus protected from chills. Horses which sweat freely at work soon lose 'condition'; the writer's observations have shown that this is due to the protein lost by the skin, for, as we shall presently see, proteins are found regularly in the sweat of the horse. Clipping largely prevents this loss, though for this purpose it is not necessary to clip a horse all over; a half-clipped body suffices. The influence of clipping on temperature is dealt with in the chapter devoted to Animal Heat.

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* 'On Palæogenetic Face-Pattern in Acroteric Piebalds.' Sir Jonathan Hutchinson, F.R.C.S., F.R.S., *British Medical Journal*, June, 1910.

Erection of Hairs.—In some animals, as for instance, the dog and the cat, the hairs are rendered erect under excitement such as anger or fear; this is due to the involuntary muscle attached to the hair follicle, and the process is under the influence of the sympathetic nervous system. The fibres for the body-hair emerge from the spinal cord by the inferior roots, pass to the grey ramus of the sympathetic chain, and run to the skin by the dorsal cutaneous nerves; the fibres for the head and neck are in the cervical sympathetic. Under the influence of cold the hairs on the horse's body may become erect, but there is no indication of this under psychical excitement, as in the case of the dog and cat. It is possible, even probable, that the prescience of a coming storm or change of weather exhibited by cattle may be due to the highly hygroscopic properties of their hair. Hair is one of the few organic substances which elongate instead of shorten as they grow moist. The effect of movement of every hair on the surface of the body may cause a mechanical stimulation of the hair-follicle nerves, and so give rise to an uneasiness which presages the coming change.

Effect of Rain.—It is astonishing the length of time horses may be exposed to rain without the skin getting wet. That it is not wet can be readily ascertained by lifting up and reversing the hair. This only applies to animals with an unclipped coat or a skin containing a liberal amount of dandruff. Both of these afford the greatest protection against rain, and this fact bears out the old-fashioned view that horses living in the open should not be too frequently groomed.

Rain causes the hairs to stand out from the surface of the body and separate into groups, which run together at the point, resembling a wet camel-hair brush. These form a series of miniature water-sheds, the rain running off the upper to the lower groups. The hair ' streams ' direct the course of the water in its passage over the body, as is well seen on the trunk, where the flanks remain dry for a considerable time. The shape of the body, especially that of the trunk, insures that the wet area is largely confined to the upper part, behaving, indeed, as a barrel would if placed on its side and exposed to rain. It takes a considerable amount of rain to wet the lower half of the trunk. When rain is accompanied by wind the whole of the windward side gets wet, and early penetration is more likely to occur.

It is not intended to suggest that horses appreciate rain; they dislike it intensely, and if given an opportunity always turn their tails to it; they shiver and shrink in size. The shivering is due to the wet coat, and not to the wet skin; the shrinkage to the fact that in wet weather much of their food is lost or even not given them. No harm arises from this exposure when animals are in health, but 'war-worn' horses may die by dozens during a wet, cold night.

The impermeability to rain of the normal coat of animals has proved a serious difficulty in dealing, by the process of 'dipping,' with the repression of mange and the eradication of tick-borne diseases. Colonel Watkins Pitchford found that, though the entire body was immersed in a solution of arsenic, this did not penetrate, owing to the protective action of the hair, and that 'ticks' consequently survived. He inhibited this by the addition of paraffin emulsion to the dressing, and in this way insured the complete wetting of the skin.

Sweat.—By means of glands in the skin a fluid termed 'sweat,' and a fatty material known as 'sebum,' are secreted. Sweat, or perspiration, is not found to occur over the general surface of the body in any other hairy animal than the horse. There are certain parts of the skin which sweat more readily than others: the base of the ears is the first place in the horse where sweating takes place; the neck, side of chest, and back follow; lastly, the hind-quarters. No sweating takes place on the legs; the fluid found there has run down from the general surface of the body. Mules and donkeys sweat with difficulty, and then principally at the base of the ears. The ox sweats freely on the muzzle, and sweating even from the general surface of the body has occasionally been observed. It has been said that sheep perspire, while it is certain that both the dog and cat, especially the latter, sweat freely on the foot-pads, as also on the muzzle, though not in the form of sensible perspiration on the general surface of the body. The sweating of the pig is confined to the snout.

The secretion of sweat is continuous. When excreted in small amounts it evaporates as fast as it is formed, passing off as the insensible vapour which is always rising from the surface of the skin, and is known as 'insensible perspiration.' When the secretion is rapid and copious or the surrounding atmospheric conditions are unfavourable to its evaporation, it collects on the skin as that visible fluid material which is ordinarily termed 'sweat.' Colin gives various numerical statements respecting the insensible perspiration, from which we gather that 6·4 kilogrammes (14 pounds) of water probably represents this loss in the horse for twenty-four hours. Much depends upon the humidity and temperature of the atmosphere; the drier and hotter it is, within certain limits, the greater the insensible perspiration.

The **amount of sweat** secreted daily can only be roughly determined; there are many conditions which affect it, such as 'condition,' length of the coat, nature of the work, and pace. Grandeau, by estimating the total water consumed in the food and drink, and that voided in the urine and fæces, arrived at the amount of vapour passing away in the breath and perspiration. The mean amount of water evaporated daily by these two channels, under different conditions of work, was as follows:

At rest	2·9 kilogrammes	(6·4 pounds).
Walking exercise	3·9 ,,	(8·6 ,,).
At work walking	5·8 ,,	(12·7 ,,).
Trotting	6·0 ,,	(13·4 ,,).
At work trotting	9·4 ,,	(20·6 ,,).

The distances walked and trotted and the loads drawn were the same. It is unfortunate that we have no means in the above experiments of determining the proportion which the water of respiration bears to that of perspiration.

Evaporation from the surface of the skin is a most important source of loss of heat; so marked is this loss in the horse that the resulting fall in temperature may even carry it below the normal if the sweating be very profuse or the wetted area a large one.

The compensating action existing between the kidneys and skin observed in man exists also in the horse—viz., when the skin is acting freely, less water passes by the kidney, and *vice versa*.

Sweat obtained from the horse is always strongly alkaline; after filtration it is the colour of sherry, which is probably accidental, and due to contamination with dandruff. The latter contains a pigment, chlorophyll. The sweat possesses a peculiar horse-like odour, and has a specific gravity of 1·020. We found it to have the following composition:*

		Containing—	
Water	94·38		
Organic matters	0·52	Serum albumin	0·105
		,, globulin	0·327
		Fat	0·002
Ash	5·10	Consisting principally of potash and soda, chlorides, some magnesia, a little lime, and traces of phosphates.	

The proteins are thus seen to be serum albumin and serum globulin, and their constant presence has been determined by a number of observations; the percentage of mineral matter is very high, and consists principally of soda and potash, especially the latter. It will be observed that the mineral matter greatly exceeds the organic matter; in horses which have sweated freely the dried, matted hair (albumin is the cause of the matting) is often seen covered with saline material, looking like fine sand. There appears to be some complemental action between the skin and the kidneys in the elimination of soda and potash; during rest the kidneys eliminate these salts, while during work they are assisted by the skin. Urea is also probably present in sweat (see p. 323). It is difficult to see why horses should excrete albumin by the skin; the loss thus produced accounts for the great reduction of vitality and strength in animals which sweat freely at work. As we have already said, clipping is the only preventive of sweating.

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* 'The Sweat of the Horse,' *Journal of Physiology*, vol. xi., 1890.

Nervous Mechanism of Sweating.—A skin may sweat under quite opposite conditions—viz., both with a hot flushed surface and with a bloodless cold one; in other words, an animal may sweat when it is hot or when it is cold. The former is a physiological condition and regulates, as we shall see, the body temperature; the latter is abnormal, but it occurs at death and disproves at once any notion of sweating necessarily depending upon a congested condition of the vessels of the skin. Experiments show that most of the features of sweating can be accounted for through the agency of the nervous system. The *sudo-motor* nerves, whose function it is to determine the secretion of sweat, are quite distinct from those which regulate the vascular supply, although they reach the nerves of supply by the same sympathetic channels as the vasomotor fibres. If the peripheral end of the divided sciatic in the cat be stimulated, the foot-pads sweat; apart from the fact that stimulation of the sciatic causes a constriction of the bloodvessels in the leg, the proof that this reaction is a specifically nervous one is easy, for the sweating still occurs when the leg has been cut off or the aorta tied, and it is absent under the influence of atropine. The effect of atropine on the sweat glands is very closely allied to its action on the salivary glands (p. 175); it paralyses the secretory nerves which stimulate sweat secretion.

As with the salivary glands, so in the present case secretion is not due to any increased supply of blood. It is true that in normal sweating, as is so readily seen in man, the skin is flushed when the increased secretion takes place, but the increased blood-supply which the flushing indicates is merely the necessary adjuvant, not the cause of the secretion; it supplies the glands with the extra material they now require, the secretory nerves causing the gland-cells to utilise the increased supply.

The secretion of sweat may be induced in man, the cat, and the dog, though not in the horse, by the injection of pilocarpine.

In this case the action is peripheral—that is to say, on the glands themselves—since it occurs when the sciatic nerves are cut previously to the injection.

As we have seen, secretion is ordinarily brought about by specific efferent nerves, and these originate in the central nervous system, from which the necessary secretory impulses are directly supplied. But secretion may also be readily induced by the stimulation of *afferent* nerves, as in the all-important case of a rise in the surrounding temperature. These facts lead at once to the belief that 'sweat centres' must exist in the central nervous system comparable to those of the respiratory and vascular mechanisms, though they have not as yet been so definitely localised. There seems to be no doubt that the spinal cord contains sweat centres. The existence of a similar centre in the medulla is less certain, though probable, since in some men perspiration over the face and neck results from merely smelling a pungent substance, such as curry-powder, and becomes profuse if the latter is introduced into the mouth.

The sweat-nerve supply to the fore and hind limbs leaves the spinal cord in company with the inferior roots of the spinal nerves, and by means of the *rami communicantes* passes to the sympathetic ganglia, and by post-ganglionic fibres reaches the brachial and sciatic plexuses respectively. The sweat fibres for the head and neck are in the cervical sympathetic; those for the face in the horse, the muzzle in the ox, the snout in the pig, run in branches of the fifth pair of nerves. Division of the cervical sympathetic in the horse produces profuse sweating of the head and neck, limited to the side operated upon; this may be due to vasomotor paralysis, though a different interpretation has been placed on it—viz., that the sympathetic carries inhibitory impulses to the sweat glands of the head, so that on division the secretory fibres act without opposition. In the ox Arloing has shown that division of the cervical sympathetic causes the muzzle on the same side to become dry; stimulation of the cut end of the nerve is followed by secretion, but this is not so when the nerve degenerates, though even then the glands respond to pilocarpine.

As previously stated, a high temperature favours the activity of the epithelium lining the sweat glands, for if the limb of a cat be kept warm, a larger secretion of sweat is obtained on stimulating the sciatic than from a limb kept cool; in the latter, stimulation of the sciatic may produce no secretion whatever. Further, if a cat in which one sciatic has been divided be placed in a hot chamber, profuse secretion will occur on the foot-pads of the limbs not subjected to interference, while on the side on which the sciatic has been divided no sweating occurs. This is a further proof of the existence of a reflex mechanism, to which we have already drawn attention. It has been thought that the sweating which takes place at death is due to a dyspnœic condition of the blood, and in many cases this may be so; perhaps dyspnœa may also account for the profuse cold sweating in ruptures of such viscera as the stomach and intestines; but it cannot explain the localised hot sweating which is often so well marked in horses between the thighs immediately after they are destroyed. Thrombosis of both iliac arteries may occur in the horse, and a frequent symptom of this trouble is the peculiarity in the accompanying sweating; the general surface of the body may sweat freely, but not the hind-quarters. In man a similar phenomenon has been met with in cases of spinal injury. The cause of this peculiarity has not been worked out.

In comparing the sweat glands with the salivary, we must be careful not to draw too close a parallel, for though in certain features they agree, in others they are very different; for instance, in the horse pilocarpine produces, as in other animals, a profuse salivary flow; but, contrary to its action on man, the dog, and cat, it has no effect whatever in producing sweating.

The peculiar breaking out into sweats which occurs in horses *after* work has no parallel in man; some animals will break out two and three times for hours afterwards, even after having been rubbed quite dry. This may be connected with the necessity for a discharge of body-heat, since the internal temperature rises above the normal during work, in some cases, it is said, as much as 2·5° to 3° C. (4° to 5° Fahr.), and remains above normal for some time afterwards. Another peculiarity in sweating of the horse is the patchy perspiration observed occasionally, such as a wet patch on the side or quarter, which dries slowly, or may remain for days or weeks, even months, in a wet or damp condition. This must be a paralytic secretion, but nothing is known of its true nature. Finally, there is no drug, so far as we are aware, which produces sweating in horses; this is perhaps an explanation of the common use of nitre in veterinary practice, the kidneys being made to do the work of the skin.

Sebaceous Secretion, or **Sebum,** is a fatty material formed in the sebaceous glands of the skin, which in the horse are freely distributed over the whole surface of the body. Though it is spoken of as a secretion, yet the process involved is not secretory, inasmuch as the cellular elements of the gland are not actively employed pouring out material, but are themselves shed after undergoing fatty metamorphosis. The greasy material thus excreted saves the epithelium from the disintegrating influence of wet, keeps the skin supple, and gives its gloss to the groomed coat; from its greasy nature it assists in preventing the penetration of rain, and thereby saves, to some extent, undue loss of heat.

Dandruff.—The material removed from horses by grooming consists of a white or grey powder which can readily be moulded by pressure into a dough-like mass; it has a curious smell, which can only be described as 'horse-like.' It consists of epithelial scales, fat, largely in the form of lanolin, colouring matter, salts, and a considerable amount of silica and dirt, the quantity of the last two depending upon the cleanliness of the animal. The amount of dandruff lost in an ordinary grooming varies from 1·25 to 3·75 grammes (20 to 60 grains) for clean horses, and 11 to 13 grammes (170 to 200 grains) for very dirty animals. An analysis of dandruff from the horse gave the following composition:*

Water -	- 17·96		
Fat -	- 12·40		
Organic matter	- 56·22	containing	1·07 of urea.
Ash -	- 13·42	,,	2·45 of silica.
	100·00		

The fatty matter in the skin proves to be lanolin, the same substance as is found in the fleece of sheep. This explains why horses living in the open should not be too freely groomed, and the reason for the prejudice which has always existed against this practice. It is evident that with free grooming the loss in fat alone is something considerable, and the animal is exposed to chill. The amount of fat lost depends upon the nature of the diet; on a purely hay diet there is very little fat in the dandruff, while on oats there is a considerable amount. The urea shown in the analysis is no doubt derived from the sweat.

Dandruff contains a colouring matter found by the writer to be chlorophyll which has undergone modification by passing from the digestive canal to the skin. The use of this pigment is unknown; in fact, the horse is the only vertebrate in which chlorophyll has so far been found as a constituent of any cutaneous excretion.

In certain places, as in the prepuce, considerable quantities of **sebum** are found. The sebaceous secretion of the prepuce of the horse consists of 50 per cent. fat, and also contains calcium oxalate. The ear-wax and the eyelid secretions are also of a sebaceous nature. In the sheep a considerable quantity of fatty substance is found in the wool; it exists in two forms: (1) as a fatty acid united to potash to form a soap, and (2) a fatty acid combined with cholesterin instead of glycerin; the latter is known as lanolin, and is largely used as a basis for ointments. It is also found in hair, horn, feathers, etc. The fatty substance in the wool is known to shepherds and others as 'suint.' In merino sheep it may amount to more than one-half the weight of the unwashed fleece, but in ordinary sheep exposed to the weather it may be 15 per cent. or less. The large amount of potash in unwashed wool is very remarkable; a fleece sometimes contains more potash than the whole body of the shorn sheep (Warrington).

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* 'Dandruff from the Horse, and its Pigment,' *Journal of Physiology*, vol. xv., 1893.

Respiratory Function of the Skin.—Certain vertebrates such as the frog can respire by the skin in the entire absence of lungs; in this way they absorb oxygen, and excrete carbonic acid. Observations made on other animals and on men have demonstrated that similar changes occur through the skin, but on a very small scale.

Varnishing the skin causes death rapidly in rabbits, and more slowly in horses. Death is due to loss of body-heat, and not to the retention of poisonous products, as was at one time supposed. Bouley* states that horses shiver when varnished, the surface of the body and the expired air become colder, the visible membranes respond by becoming violet in tint, and the animals die after several days. According to Ellenberger, if only partly varnished they do not die, but exhibit temporary loss of temperature, and show signs of weakness. The effect of varnishing the skin is to cause the capillaries to dilate, and so produce a great discharge of heat.

For absorption from the skin, see 'Absorption,' p. 290.

The **Chestnuts** and **Ergots** are considered to be the remains of hoofs belonging to digits long since lost by the horse. The ergot grows from the back of the fetlock; the chestnut is found on the inside of the arms and hocks, and is always larger in the former position. In the heavy type of horse they may grow to a considerable size. The horn of which they are composed is tubular in structure, and produced by the papillæ of the skin. After attaining a certain size they drop or are pulled off. Both ergots and chestnuts are found larger in horses wanting in quality than in those better bred; in the donkey and the mule the chestnut forms no outgrowth of horn, but a hairless black patch represents its position.

Pathological.

The chief pathological conditions of the skin are those due to parasitic invasions; these may produce widespread disease in all animals.

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* Colin's 'Physiologie Comparée.'

CHAPTER X

THE URINE

The urine is sometimes spoken of as a secretion, but this is not strictly correct; speaking broadly, it may be said that a secretion is something which is formed in a part for the purpose of being eventually utilised by the system. This does not apply to the urine, the chief constituents of which are not even prepared in the kidneys, but only separated by them; moreover, the urine, having once been formed, is of no further use to the body, and is excreted. An excretion, therefore, is something removed from the system as no longer required, and the retention of which would be harmful. Such a removal is effected by the kidneys, which may in a sense be regarded as the filters of the body, regulating the composition of the blood by removing from it waste and poisonous products, and maintaining in it, as will be later explained, the proper degree of chemical neutrality.

The method adopted by the kidney for the secretion of urine has been for many years one of the chief subjects for physiological dispute. These very vascular glands are capable of separating from the blood a fluid which is essentially different in composition from the blood itself. The blood is faintly alkaline in reaction, the urine acid or alkaline, depending on the class of animal; the blood is an albuminous fluid, the urine in a state of health is free from protein; the blood contains sugar, the urine contains none; the blood has one colouring matter, the urine another; the blood contains urea and salts in small quantities, the urine contains them in relatively large amounts; the blood maintains the whole of its inorganic material in solution or in such a form as to be readily soluble, the urine may be of such concentration or reaction as to be unable to retain its substances in solution. Nevertheless, the kidney only takes from the blood what is brought to it, for, with the single exception of hippuric acid, none of the urinary constituents are formed in the gland. There is no other body secretion which exhibits such striking differences, and, further, there is no other gland the structure of which resembles the peculiar histological structure of the kidney.

The vascular arrangements of the kidney are intimately connected with the function of the organ. The renal artery is short, it comes off close to the posterior aorta, and the pressure within it is practically the same as in that vessel; the pressure in the renal vein, on the other hand, is low—nearly as low as that in the posterior vena cava. It will be observed that the same amount of blood-pressure as is required to fill the vessels of the lumbar region and hind-limbs is expended on driving the blood through the kidneys. At every increase in the amount of blood in the kidney the organ swells, at every decrease it contracts. These movements on the part of the kidney have been carefully studied by means of Roy's *oncometer* or similar plethysmographs. An oncometer (Fig. 94) is a metallic capsule in which the living kidney is enclosed, so arranged that the expansion and collapse of the organ can readily be recorded. A tracing made by this instrument shows that the volume of the kidney is affected by every beat of the heart, and even by the respiratory undulations in the blood-pressure.

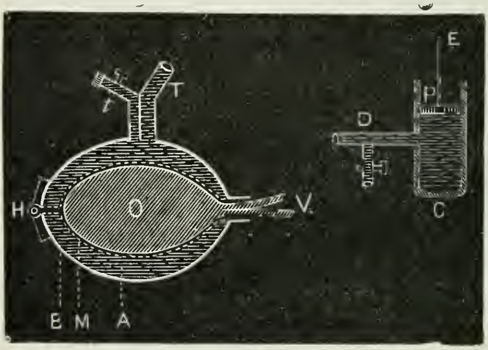


Fig. 94.—Diagram of Oncometer.

B, Metal box in two halves, opening on the hinge H; M, thin membrane; A, space filled with oil; O, organ enclosed in oncometer; V, vessels of organ; *t*, tube for filling instrument with oil; T, tube connected with D, which opens into cylinder C; P, piston attached by E to writing lever.

Structure of the Kidney.—The kidney consists of a central part, the medulla, surrounded by an external part, the cortex; the boundary of the two is easily visible in a sliced kidney. The branches of the renal artery break up at the boundary of the cortical and medullary portions. The cortex of the kidney is the essential secreting region, and it is here that the *Malpighian tufts* or *capsules* are found. These consist of small clusters of capillaries, the *glomeruli*, derived from the renal artery. The afferent arteriole entering the glomerulus is larger than the efferent or outgoing one, and as in addition the blood passing from the efferent vessel has to pass through a second set of capillaries supplying the *uriniferous tubules*, a high blood-pressure is maintained within the glomerular capillaries. The glomerular tuft invaginates the blind end of the uriniferous tube, the inner layer of the dilated end being separated from the outer layer (Bowman's capsule) by a space into which the urinary filtrate passes. Dilatation of the capillaries diminishes this space, while it is enlarged by their collapse. Fig. 95 shows the general arrangement of the Malpighian bodies, and Fig. 96 that of the vessels in a tuft. The minute vein or efferent vessel leaving the tuft breaks up into capillaries around the uriniferous tubule; thus the blood in the plexus of capillaries around the tubule is derived from two sources—viz., from the tuft, and directly from the renal artery. The capsule of Bowman, which surrounds the tuft, is lined with cells resembling the epithelioid plates seen in capillaries; they are flat polygonal cells contain-

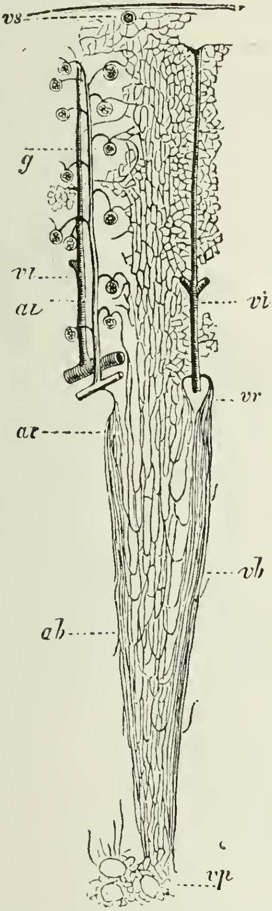


Fig. 95.—Diagram of Bloodvessels of Kidney (Klein, after Ludwig).

ai, Interlobular artery; *vi*, interlobular vein; *g*, glomerulus with its afferent and efferent vessels, the latter breaking up into a plexus around the renal tubules; *vb*, venæ rectæ; *ar*, arteriæ rectæ; *vp*, apex of papilla; *vs*, vena stellata (Stewart).

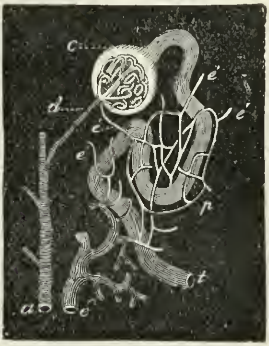


Fig. 96.—Diagram showing the Relation of the Malpighian Body to the Uriniferous Tubules and Bloodvessels (Kirke, after Bowman).

a, An interlobular artery; *a'*, branch of artery passing into the glomerulus; *c*, capsule of the Malpighian body forming the commencement of, and continuous with *t*, the uriniferous tube; *e'e'e'*, vessels leaving the tuft forming a plexus, *p*, around the tube, and finally terminating in *e*, a branch of the renal vein.

ing a nucleus. The capsule is practically the dilated beginning of a uriniferous tubule, and the latter is continued from the capsule, taking a course of extraordinary complexity to the pelvis of the kidney; but the cells found in the tubule are no longer the flat polygonal cells of the capsule; they are special to the tubule, and even to different parts of it (Fig. 97).

If the course of a uriniferous tubule is briefly followed (Fig. 98), it is found that on leaving the capsule it becomes twisted in the cortex, forming the *convoluted tube ;* it then forms a *spiral tube,* and leaving the cortex, runs straight into the medulla, forming the *descending limb of Henle ;* it now makes a sharp turn, the *loop of Henle,* and travels back to the cortex, in the same way that it left, by the *ascending limb of Henle.* The descending limb is straight and narrow, the ascending limb is wavy in character and larger. Having reached the cortex, the ascending limb becomes distinctly wider and twisted, forming the *zigzag* or *irregular tubule ;* from this a tubule is continued which resembles in its contortions the first convoluted portion; it is termed the *second convoluted tubule.* This now leaves the cortex and enters the medulla as a straight tube, known as the *collecting*

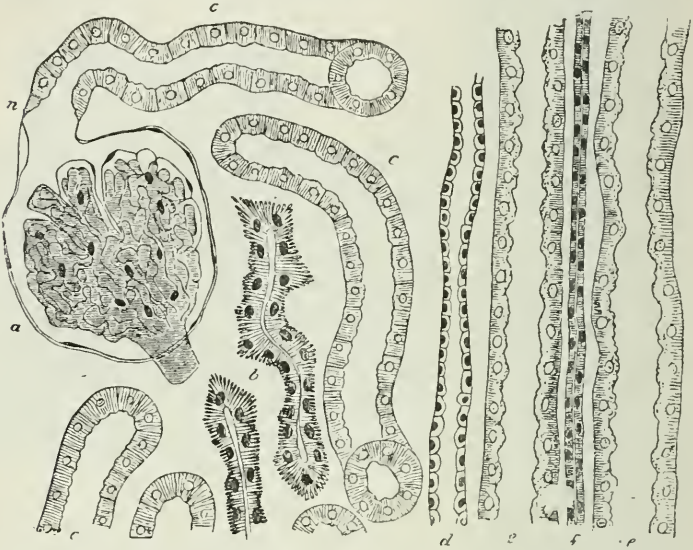
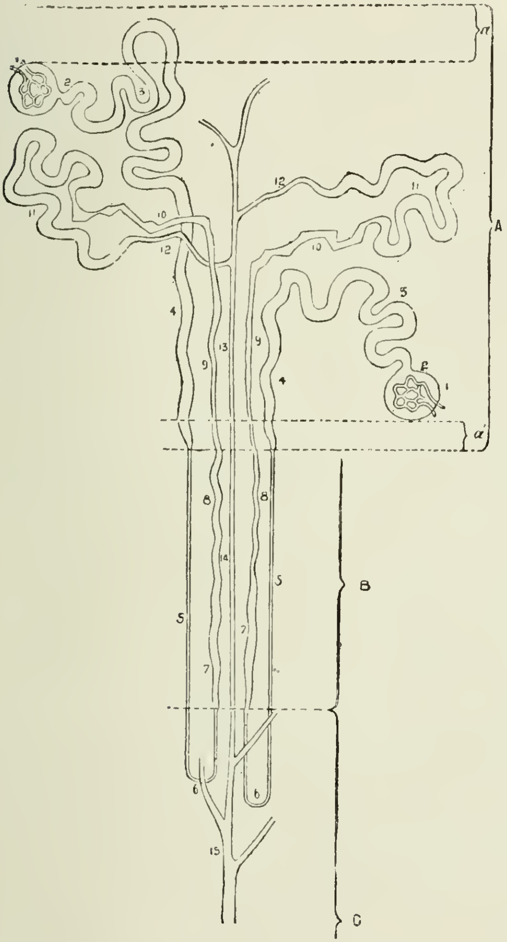


FIG. 97.—FROM A VERTICAL SECTION OF THE DOG'S KIDNEY, TO SHOW THE STRUCTURE OF THE DIFFERENT PORTIONS OF THE RENAL TUBULE (KLEIN).

a, Bowman's capsule enclosing glomerulus; *n*, neck of capsule; *c c*, convoluted tubes cut in various directions; *b*, from zigzag tubule; *d*, from collecting tubule; *e e*, from spiral tubules; *f*, narrow part of Henle's loop tubule. In *b*, *c*, and *e*, 'rodded' epithelium is seen (Stewart).

tube; it runs towards the apex of the pyramid, and joins other collecting tubes; by so doing it becomes larger, and on reaching the apex is known as a *discharging tube* or *duct of Bellini.* The epithelial cells lining the tubules are not of the same character throughout; broadly, they may be divided into striated or 'rodded' cells, staining readily, and clear transparent cells, staining with difficulty. The 'rodded' epithelium is suggestive of secreting cells, and is found in the two convoluted tubules



A, Cortex of kidney; *a*, subcapsular layer not containing glomeruli; *a′*, inner structure of cortex also without glomeruli; B, boundary layer of medulla; C, papillary part of the medullary; 1, Bowman's capsule of the glomerulus; 2, neck of capsule; 3, proximal convoluted tube; 4, spiral tube; 5, descending limb of Henle; 6, loop of Henle; 7, thick part of ascending limb; 8, spiral part of ascending limb; 9, narrow ascending limb in the medullary ray; 10, the irregular tubule; 11, distal convoluted tube; 12, curved collecting tube; 13, straight collecting tube; 14, collecting tube of boundary layer; 15, large collecting or discharging tubule of papillary layer.

FIG. 98.—DIAGRAM OF THE COURSE OF THE URINIFEROUS TUBULES (KLEIN AND NOBLE SMITH).

and in the spiral and zigzag tubules (Fig. 97); the clear cell, on the other hand, partakes more of the characteristics of the epithelial lining of ducts.

Vascular Mechanism.—The vascular arrangements of the kidney are under the control of a rich supply of vaso-constrictor nerves, and dilator nerves are also known to exist. If the general blood-pressure be constant, dilatation of the renal vessels means an increased secretion of urine, while constriction of the vessels means a reduced secretion. An increase in the general blood-pressure produces an increase in the amount of blood in the kidney, and this is rendered evident by the swelling of the organ in the oncometer and an increased production of urine. If the increased general blood-pressure is accompanied by a *constriction* instead of a dilatation of the small arteries of the kidney, as, for instance, when the vaso-constrictor nerves are stimulated, then the increased blood-pressure cannot lead to increased secretion, but, on the contrary, the amount of urine becomes less and the kidney *shrinks*. A fall in general blood-pressure, such as is caused by dividing the spinal cord, brings about a reduction in the flow through the kidney, and the blood-pressure becomes so low that the secretion of urine is entirely suspended. It is thus evident that the vasomotor influence over the kidney is of the greatest importance, and largely regulates the amount of urine excreted. If the renal vein be obstructed, the pressure of blood in the kidney rises, but no urine is secreted; evidently, therefore, a continuous flow of blood through the kidney is as essential to secretion as is increased blood-pressure.

The **Theories of Urinary Secretion** are at least three in number. One put forward by Bowman regarded the epithelium of the glomerulus as the seat of secretion of the water and inorganic salts of the urine, while the epithelium in the convoluted tubules was considered to secrete the urea and other organic substances. The view is essentially secretory, and is opposed to the theory formulated by Ludwig, which is wholly mechanical in character. Ludwig regarded the glomerulus as forming the entire urinary constituents under the influence of pressure brought about by the peculiar structural arrangements of the part. In the glomerulus, according to this view, a highly diluted fluid was formed which, in its passage to the pelvis of the kidney, was exposed to *absorption* by the epithelial cells, by which means it became concentrated. The majority of physiologists, at least until recently, accepted the Bowman theory.

If the whole process of urinary secretion were a question of pressure in the glomerulus, then ligature of the renal vein should result immediately, though not continuously, in a greater secretion of urine. As a matter of fact, we know the secretion ceases.

This experiment seems a very crucial one. The fact of closing the venous outlet must greatly raise the capillary pressure, and favour in a remarkable manner the passage of fluid by filtration, yet none is filtered off. Ludwig explained the diminution in secretion after constriction of the renal vein as being due to the distended veins compressing the tubes in the medulla, and so preventing the passage of the fluid to the ureter. Even if this were not the explanation of the anuria, such constriction of the vascular path from the stoppage of the arterial blood-supply would produce asphyxial conditions which must affect the condition of the filtering membrane, as is evidenced by the appearance of albumin and casts in the urine. It is now recognised that the experiment does not disprove the rôle of the glomerulus in filtration. Many experiments have been made to prove the secretory activity of the cells of the convoluted tubes; the one by Heidenhain was at one time regarded as conclusive.

If sulphindigotate of soda be injected into the blood of the dog, within a short time the urine acquires an intensely blue colour, though the blood may be only slightly affected. If the kidney be removed and examined, all parts excepting the Malpighian bodies are found stained blue. In order to determine what portion of the tubule excretes the dye, it is necessary to stop the secretion in the glomeruli, otherwise the colouring matter gets carried through the whole length of the tubule. In order to stop glomerular secretion, the blood-pressure is lowered by dividing the spinal cord in the neck, and the blue colouring matter is then injected, and the kidney subsequently examined. The blue is now found in the cortex only, and within the striated or rodded epithelial cells of the first and second convoluted tubes, in which the pigment may be seen lying in granules. From this experiment it is clear that the cortical tubules elected to turn out the pigment from the blood, while the medullary tubules were unable to effect this. It is therefore fair to assume that a specific secretory activity of the cells of the convoluted tubes is shown for indigo, and it is assumed that a similar function may be exercised towards other bodies—for instance, urea and the other constituents of the urine. Some investigators hold that the pigment seen in the tubes is in process of being absorbed, not secreted.

Stated briefly from the point of view of secretion, these facts amount to this, that in the glomeruli the water of the urine—and perhaps the salts—are passed out chiefly as the result of varying glomerular blood-pressure, while the organic matter is excreted in the tubules as the result of the distinctly secretory activity of their cells. These substances are carried along by the fluid which trickles down the tubules into the pelvis of the kidney, and so becomes urine. Secretion of protein in the tuft, and its reabsorption in the tubule, was at one time believed to take place, but inasmuch as no protein is found in the normal urine of any animal, it is safe to assume that in an undamaged state the epithelial cells of the glomerulus allow none to pass. Under pathological conditions the glomeruli permit the exit of both albumin and sugar. There are no secretory nerves to the kidney; the influence of the nervous system is here confined to its action on the bloodvessels, and thus to regulating the flow of blood through the kidney.

Brodie regarded the glomerular activity as secretory,* and considered that the high blood-pressure in the glomerulus was the propelling force which drove the urine secreted by the tubules through their very long and narrow passages. He proposed to call the glomerulus a 'propulsor,' and pointed out that the kidney during activity was tense, hard, and distended its capsule to the utmost. The importance to the kidney of a firm inextensible capsule had not previously been insisted upon.

The 'Modern' Theory.—Recently (1917) attention has been again directed to this subject by Cushny.† The position which this writer takes up is a somewhat different one from that adopted by Heidenhain on the one hand, and Ludwig on the other. According to this theory, there filters through the glomerular capsule simply deproteinised plasma, the filtrate therefore containing all substances other than proteins in the concentrations in which they exist in the plasma. Such a filtrate must not only be much more dilute than urine, but must also contain substances which are not normally present in the urine. The theory, therefore, necessitates the absorption of a large quantity of fluid by the tubes, and also of many of the dissolved constituents of the filtrate, to such an extent as to bring the final fluid as it enters the ureters to the normal composition of urine.

The absorbed fluid, for example, would require to contain all the glucose which had filtered through the glomerulus, in the concentration in which this body occurs in the plasma. In the case of an acid urine the excess alkali which had passed through, would also require to be absorbed as well as chloride, sodium, and potassium, approximately in the proportions in which these last three exist in the plasma.

Such a fluid would be similar in some respects to Locke's fluid as used in perfusion experiments. The following table from Cushny's monograph explains clearly the nature of the process concerned in the excretion of 1 litre of urine:

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* 'Glomerular Activity,' Proceedings of the Royal Society, June 15, 1911. Dr. T. G. Brodie, F.R.S.

† 'The Secretion of Urine,' 1917. Professor A. R. Cushny, F.R.S.

	67 Litres Plasma contain—		62 Litres Filtrate containing in all—	61 Litres Reabsorbed Fluid contain—		1 Litre Urine contains—	
	Per Cent.	Total.		Per Cent.	Total.	Per Cent.	Total.
Water	92	62 l.	62 l.	—	61 l.	95	950 c.c.
Colloids	8	5,360 gr.	—	—	—	—	—
Dextrose	0·1	67 gr.	67 gr.	0·11	67 gr.	—	—
Uric acid	0·002	1·3 gr.	1·3 gr.	0·0013	0·8 gr.	0·05	0·5 gr.
Sodium	0·3	200 gr.	200 gr.	0·32	196 gr.	0·35	3·5 gr.
Potassium	0·02	13·3 gr.	13·3 gr.	0·019	11·8 gr.	0·15	1·5 gr.
Chloride	0·37	248 gr.	248 gr.	0·40	242 gr.	0·6	6·0 gr.
Urea	0·03	20 gr.	20 gr.	—	—	2·0	20 gr.
Sulphate	0·003	1·8 gr.	1·8 gr.	—	—	0·18	1·8 gr.

From 'The Secretion of Urine,' p. 48, by A. R. Cushny.

The action of diuretics has been studied in connection with the question of urinary secretion, and the general outcome of the work is that these effect their purpose either by increasing the flow of blood to the kidneys, or by directly stimulating the secretory activity of the cells.

The function of the cells of the tubules does not end with the removal from the blood of the substances presented to them; they are also capable of forming new material. Thus the union of glycine with benzoic acid, resulting in the formation of hippuric acid, takes place in the cells of the tubules, and observations have shown that, providing the benzoic acid be presented to it, the kidney is capable of furnishing the needful glycine. It can hardly be doubted that what is true of glycine and benzoic acid may also be true of other substances, and that in the cells transformations may occur which lead to the production of colouring matters, etc., and of which our knowledge is at present obscure. Mucin, so prominent a feature in the urine of the horse, must also be prepared by the cells of the tubules, or those of the pelvis of the kidney, as being a colloid it cannot escape through the glomerulus by filtration.

The Composition of the Urine.—The urine contains nearly the whole of the waste nitrogenous, some of the non-nitrogenous, and the greater part of the saline products of the body, the difference being made up by the skin, especially in the horse, where, we have already seen, protein, urea, and salts are to be found in the sweat. We have yet to study the complex subject of tissue disintegration; nevertheless, to enable a clear perception to be formed of the physiology of urinary secretion, it is necessary to very briefly state some of the essential facts in order that the functions of the kidney may be appreciated.*

The blood passing through the kidneys carries with it the disintegrated products of the tissues and of those substances of the food which have been absorbed. It is not possible to state precisely what proportion of the urinary products are due to changes in the tissues, and what proportion to the breaking down of food substances which have formed no part of the tissues. Whatever their source, by the time they are excreted in the urine they are waste products and incapable of further use by the system. Speaking broadly, the kidneys form the path by which the end products of the disintegration of protein food and inorganic salts obtain exit from the body, while those of non-protein food are eliminated mainly by the lungs, a small proportion being dealt with by the kidney in herbivora. It is, therefore, the all-important protein which mainly concerns us in connection with the urine; the exceedingly complex protein molecule, whether it be that which has formed part of the tissues, or that immediately derived from the food and not yet built into the body structure, is broken down step by step into simpler bodies, which when the end products are reached are eliminated from the blood through the kidneys. The simplicity of these end products may be judged from the fact that, though protein has never yet been obtained in a pure condition, and its molecular structure is therefore unknown, it is certain that its molecular weight is very high. It is believed, for example, that the molecular weight of a globulin known as *edestin*, obtained from hemp-seed, is approximately 14,500, while its end products in the urine, after the system has been chemically tearing it to pieces, would contain only 8 atoms if eliminated as urea, or 22 atoms if eliminated as hippuric acid.

The composition of the urine varies with the species of animal. In all herbivora the secretion, with certain minor differences, is much the same; omnivora and carnivora each possess a distinctive urine; in all cases the differences are explained by the character of the food. When herbivora live on their own tissues, as during starvation, or under pathological conditions, they become carnivora, and their urine alters in character, corresponding now to that of flesh-feeders. Similarly, the young of herbivora, while still sucking, have a urine possessing much the same characteristics as that of carnivora.

In amplification of these general statements it is necessary to point out that in animals of the same class the composition of the urine may vary within very wide limits in accordance with several causes, of which diet is the most important.

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* The student is advised to read the chapter on Nutrition in conjunction with that on the Urine, as the subjects are largely complemental.

Urine consists of—

Water.	
Organic matter -	Nitrogenous end-products: urea, uric acid, allantoine, hippuric acid, creatinine. Aromatic compounds: benzoic acid, ethereal sulphates of phenol, cresol, etc. Non-nitrogenous substances (herbivora) of unknown origin. Colouring matter and mucus.
Salts - -	Sulphates, phosphates, chlorides, and carbonates of sodium, potassium, calcium, and magnesium.

Nitrogenous End Products.—The total nitrogen of the urine consists of—

1. *Urea nitrogen.*
2. *Uric acid nitrogen.*
3. *Ammonia nitrogen.*
4. *Creatinine nitrogen.*

Urea, or carbamide, is the substance in urine in the form of which the greater part of the nitrogen is got rid of: 1 gramme of protein yields $\frac{1}{4}$ gramme of urea. It is a substance very soluble in water and crystallises readily, the crystals melting on heating and giving off ammonia. In the urine it exists in a free condition, but is capable of forming salts with acids. These yield typical crystalline formations—*e.g.*, octahedra, with nitric acid (see Fig. 99)—by which they can be identified microscopically. Under the influence of an enzyme, *urease*, liberated from the *Micrococcus ureæ*, urine, on standing, becomes ammoniacal, owing to the breaking up of the urea into ammonium carbonate. This sometimes occurs in the bladder under pathological conditions. Urea is found in blood in proportions which vary between 4 and 6 per 10,000; in the urine it exists in the proportion of 300 parts to 10,000. It is only because of the continuous flushing of the kidneys with blood that this amount of urea is separated, and the size of the stream may be judged by the fact that a dog weighing 35 kilogrammes (77 pounds) has 300 kilogrammes (660 pounds) of blood streaming through the kidneys

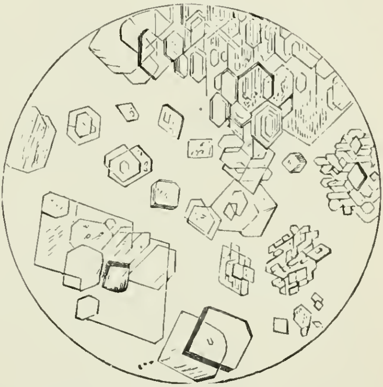

FIG. 99.—CRYSTALS OF NITRATE OF UREA.

every twenty-four hours. The urea is separated in the glomerulus by filtration, and the peculiar selective power of the cells of the tubules cannot be better exemplified than in their rejection of urea, as it streams along towards the pelvis of the kidney, and their absorption of sugar.

It is evident that the disintegration of protein material which leads to the formation of urea may be occurring in the actual protein of the tissues (*endogenous* production), or it may be taking place in the protein substances absorbed from the intestinal canal which are not part of the tissues. This is known as *exogenous* production. It is not possible to say exactly how much is contributed from each source, but it would seem that the major portion is furnished by the protein food substances not yet built into the protein of the tissues.

The history of urea is still very incomplete, but it is now generally accepted that it is formed, though perhaps not exclusively, in the liver, and that the kidneys are only its path of excretion. The form in which the antecedents of urea arrive at the liver is not definitely known, nor, indeed, are the various stages existing between protein and urea agreed upon. We have seen (pp. 195, 262-264, 334) that the protein molecule, under the influence of pepsin, trypsin, and erepsin, is gradually reduced from complexity to simplicity, and in this process its nitrogen appears as ammonia, monamino-acids, and diamino-acids. There is no reason to doubt that what occurs in the intestinal area in the breaking up of the protein molecule may also occur in the tissues. Muscles, for example, contain ammonia in large quantities. Ammonia is formed in the body tissues by intracellular ferments, and is carried by the blood to the liver. The form in which it is carried is not agreed upon, but as the ammonia in the tissues unites with carbon dioxide, it is probably carried either as ammonium carbamate or carbonate. In the liver the conversion of this into urea by the loss of water is easy to understand. The latest view is that ammonium salts reach the liver in the form of ammonium lactate. Ammonium lactate is formed by the sarcolactic acid of muscle metabolism uniting with the ammonium of the protein, and this in the liver is oxidised into ammonium carbonate, the ammonium carbonate being converted into urea. If the blood of the portal vein be experimentally compelled to pass into the posterior vena cava without circulating through the liver, the output of urea is decreased, while the ammonia compounds in the blood increase and cause poisoning. The blood of the portal vein is found to contain three or four times more ammonia compounds than arterial blood, and there can be no doubt that these highly poisonous compounds are converted in the liver into the less poisonous urea. It is well known that monamino-acids, resulting from protein disintegration, such as *leucine, glycine,* and *aspartic acids,* may be converted into urea, and it is most likely that this change is effected during their passage through the liver. The diamino-acids, represented in the body by *histidine, lysine,* and *arginine,* are also capable of conversion into urea. Arginine, for example, is acted upon by the ferment *arginase,* which is found in the liver, kidneys, and other organs, and converted into urea and ornithine (diamino-valerianic acid). No arginase is found in muscle.

It is believed that the larger part of the urea excreted is not produced by the metabolism of tissue protein, but is derived from the products of food absorption, and these are mainly represented by the ammonia compounds taken up from the intestinal area. The urea contributed by the tissues may also be represented by ammonia compounds and monamino-acids, and perhaps by the splitting up of arginine. It has been found that when the liver is removed urea does not disappear from the urine, and it is supposed that the origin of this portion is in the tissues, though this urea may not necessarily be formed in the same way as the liver urea, nor from the same material. Uric acid has by some physiologists been considered a possible source of urea, for it has been observed in man that about one-half of the uric acid produced is not excreted as such, but is got rid of as urea; in dogs, however, only one-twentieth undergoes this conversion. This change is effected by a uricolytic ferment found in the liver and other organs. Uric acid given by the mouth is excreted as urea, and outside the body it is readily converted into urea by oxidation; nevertheless, this is not very strong evidence in favour of the existence of uric acid conversion in the living body. Creatinine was at one time regarded as a source of urea, but with a better knowledge of this substance and of creatine, the conversion of creatinine into urea, which offers no difficulty as a laboratory process, is regarded in the living body as improbable.

The proportion of urea in urine varies according to the nature of the diet. In man and the dog the larger the amount of nitrogen in the food the more urea excreted, but in herbivora it has been observed that on a diet consisting principally of hay more urea is excreted than on one of oats and hay. The amount of urea excreted was at one time considered to be a measure of the amount of work performed by the animal body, but this view has long been known to be wrong, though there can be no doubt that under the influence of work rather more urea may be excreted than during rest.

Apart from these marked causes of variation there are others, which certainly in the case of the horse lead to great fluctuations in the amount of the daily excretion, even under identical conditions, of work, food, and rest. We shall see also that this is so in the dog, an animal in which occur the widest variations in the urea. In the horse, about 100 grammes ($3\frac{1}{2}$ ounces) daily is a mean excretion. The percentage of any substance in urine conveys no information unless the total amount of excretion for the twenty-four hours has been ascertained. Nevertheless, it is usual to speak of the percentage of urea and other substances, and it is a useful expression if the other data be known. In all animals the urea varies from 2·5 to 4 per cent.

Creatine and Creatinine.—Creatine is found in muscular tissue, and the amount, generally under 5 per cent., may be doubled by severe exercise or prolonged starvation. It is not regarded as a normal constituent of the urine excepting in the bird. If administered to dogs by the mouth, it appears in the urine as creatinine; if given to rabbits, as representing herbivora, only a minute proportion is recoverable as creatinine, while the remainder cannot be recovered in any form. Indeed, there are some who consider that the creatine of muscle is not converted into creatinine in the urine, but that creatinine is formed in the liver as the result of protein metabolism, then passed to the muscles, where it is stored up as creatine, the excess being got rid of by the urine as creatinine. In flesh-feeders a portion of the urinary creatinine is derived from the food, though it continues to be excreted on a meat-free diet; if a diet be given in which the proteins are reduced in amount, the creatinine is increased. The source of creatinine is unknown, though Thompson found that when *arginine*, a body chemically related to creatine, and present in most articles of diet, was injected subcutaneously into ducks it gave rise to an increased formation of creatine. The elimination of creatine in diabetic subjects has been attributed to a deficiency of carbohydrate in the body, but it is said that pigs fed on maize or oats, though containing adequate carbohydrate, excrete large quantities of creatine, and the urine becomes acid. It is believed by F. P. Underhill, to whom these observations are due, that there is an inter-relationship between acidosis and creatine elimination, and that if the acid state of the urine be abolished the excretion of creatine ceases. J. B. Orr urges that creatine is formed in relatively large quantities by ruminants, that it is utilised in the tissues, and that its utilisation is intimately connected with the metabolism of carbohydrate, the creatine formed being in inverse proportion to the amount of carbohydrate in the diet.

Creatinine occurs in the urine of all mammals. In man the amount varies with different people, yet it is so constant for the individual that the total quantity of urine secreted may be calculated from the creatinine found. Creatinine may be found in muscle, probably as the result of post-mortem conversion of creatine; it also is a regular constituent of the cereals.

Uric Acid.—This is the chief end-product of protein metabolism in birds and reptiles. It is manufactured in the liver by synthesis from ammonia and lactic acid, and excreted as acid ammonium urate. In contrast to urea, it is a substance very insoluble in water, but soluble in alkaline solutions and in alkaline phosphates. With the latter an acid urate of the alkali is formed, and acid sodium phosphate results, which gives the reaction to the urine of the carnivora. In the mammal it is known that the chief source of uric acid is not synthesis, as in the bird, but the splitting up and oxidation of a special group of protein substances known as nucleo-proteins. These bodies may be derived from the food, or from the tissues, as we have seen is the case with urea. In man food rich in nuclein, such as thymus, pancreas, and herring roe, and in purin bases as meat extract, increases the amount of uric acid produced. Uric acid (Fig. 100) does not exist in the urine in a free state, but as urates of soda or potash. Two classes of urates are formed—neutral and acid. The acid sodium urate is the chief constituent of the reddish deposit of urates which occurs in acid urines.

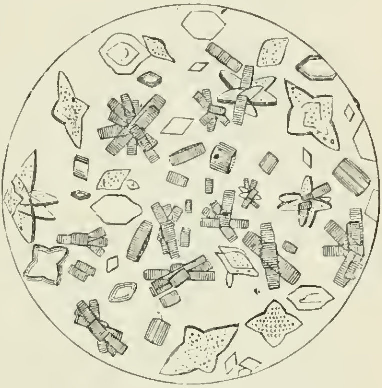

FIG. 100.—CRYSTALS OF URIC ACID (FUNKE).

We have referred to purin bases as forerunners of uric acid, and a word in explanation is necessary. Purin is the name given by E. Fischer to the nucleus common to the uric acid group of substances; from this nucleus, by transformations, several members of the group may easily be obtained. They are found in both animals and plants.

The purin group consists of the following bodies:

Purin Bodies.
- Purin Bases.
  - *Hypoxanthine.*
  - *Xanthine.*
  - *Adenine.*
  - *Guanine.*
- Uric Acid.

From the purin bases uric acid is probably formed by the following process: Under the influence of ferments the nuclein is split off from the protein and acted upon by a tissue enzyme known as *nuclease*. This splits the nuclein, and results in the formation of the above-named *purin* bases. Adenine and guanine, under the influence of tissue enzymes, are converted into hypoxanthine and xanthine, and these bodies, on being acted upon by an *oxidase* ferment, are oxidised to uric acid. Of the uric acid so formed, a portion under the influence of a uricolytic ferment is, as previously noted, converted into urea.

The uric acid problems have been worked out mainly on the dog, apart from the work done on birds. In the case of the non-suckling herbivora, it is known that in a condition of health uric acid is not found, or only to a trifling extent. It is present in the suckling, also in the adult, immediately the animal begins to live on its own tissues, as in disease. It appears clear that a flesh diet, especially of cellular organs such as the various glands, favours its production, while a vegetable one either inhibits its formation or else destroys it, perhaps in the liver, under the influence of a body ferment, producing urea in its stead. This, however, is pure conjecture. In dogs it is said that *allantoine* takes the place of uric acid.

Allantoine is an oxidation product of uric acid, and was first found in the allantoic fluid of the cow. It has been found in the urine of several of the herbivora—cattle, sheep, and rabbits—and in carnivora, as represented by the dog. Whenever found in urine it is derived from uric acid.

Hippuric and Benzoic Acids are conveniently considered together, though benzoic acid belongs to the aromatic series and contains no nitrogen. These acids are characteristic of the urine of herbivora; in man and carnivora they are found only in small amounts, in birds they are absent. Hippuric acid is formed by the union of glycine with benzoic acid, glycine being derived from the breaking down of the protein of food. The seat of the synthesis is only imperfectly known. It has been ascertained by experiments on the dog that it may be effected in the kidney, so that hippuric acid is one of the few substances capable of being formed by that gland; in the rabbit, and probably other herbivora, the synthesis may occur in the liver, as the rabbit can form hippuric acid after the removal of the kidneys. The synthesis of benzoic acid and glycine may readily be brought about outside the body by using ground-up kidney tissue mixed with blood and kept at the body temperature. If the kidney be perfused with a mixture of blood, glycine, and benzoic acid, its epithelial cells must be undamaged in order to obtain hippuric acid. This suggests that the active agent in the synthesis is an enzyme. The source of the necessary benzoic acid in not completely known. Hay, grass, and grain contain in the cuticular covering aromatic substances which yield hippuric acid in the body. It is possible to remove this cuticular covering by a laboratory process, and food so fed yields no hippuric acid.

When no benzoic acid exists in food, hippuric acid may be formed from aromatic compounds containing the benzoyl radicle derived from protein putrefaction in the intestines (Armsby).* This authority, however, draws attention to the fact that the food of herbivora does not contain sufficient of the aromatic series which yield benzoic acid to account for the amount of hippuric acid produced, especially in cattle. He states that search has been made among the non-nitrogenous constituents for an explanation of the riddle, and that investigations suggest the *pentose carbohydrates*† of the food as having some connection with the formation of benzoic acid. If cherry gum be added to the food of sheep, a marked increase in hippuric acid occurs, though this is less evident in the case of the horse.

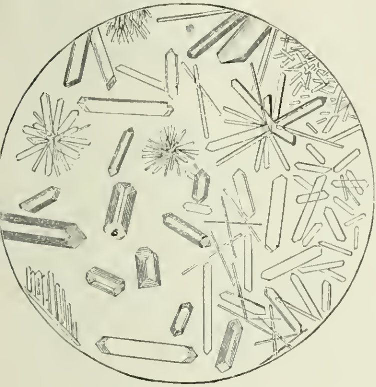

FIG. 101.—CRYSTALS OF PURIFIED HIPPURIC ACID (FUNKE).

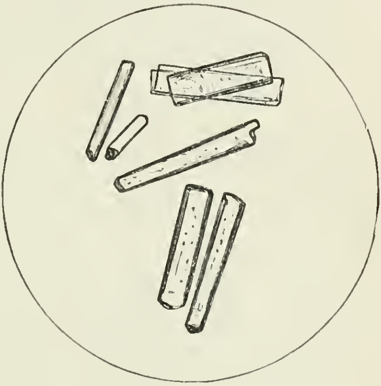

FIG. 102.—CRYSTALS OF IMPURE HIPPURIC ACID.

Neither hippuric nor benzoic acids exist free in the urine, but combined with bases, especially potash. There is in consequence, especially in ruminants, a heavy drain on the bases of the body.

Liebig, many years ago, stated that benzoic acid was found in the urine of working horses, and hippuric acid in the urine of those at rest. Our observations show that hippuric acid is generally found in the urine of working horses, and seldom found in the urine of horses at rest—in fact, the reverse of Liebig's view. Owing to its easy and rapid fermentative decomposition, hippuric acid is rarely to be found in urine twenty-four hours old; out of fifty-four specimens examined, we found it in only eight. It, however, always appears to be present in the urine of cattle. Diet plays an all-important part in the production of hippuric acid; it is increased in quantity by grass, hay, and straw feeding, and decreased by the use of clover, peas, wheat, and oats. The amount of hippuric acid excreted by horses depends, therefore, upon several factors:

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* 'The Principles of Animal Nutrition,' 1914. H. P. Armsby, Ph.D., LL.D., United States Department of Agriculture.

† These are *ribose*, obtained from the nucleic acid of plants; *arabinose*, from gum arabic, cherry gum, etc.; *xylose*, from wood gum, straw, and cellulose.

On an exclusive grass diet a horse will excrete, on an average, 120 grammes daily (4·2 ozs.).
On an exclusive hay diet, 50 grammes daily.
On a diet of hay, oats, and straw, 85 grammes daily.
On a mixed diet the amount may be 60, 140, or 165 grammes daily.

In sheep, urea stands to hippuric acid in the proportion of 2 to 3, whereas in cattle on the same diet the proportion is 2 of urea to 1·1 of hippuric acid. The food most productive of hippuric acid in the horse is old meadow hay, whilst *new* meadow hay has this effect on sheep.

With the usual caution regarding urinary percentages—viz., that they are worthless unless the total amount of secretion is known—it may be said that hippuric acid in the horse exists in the proportion of from ¾ to 2 per cent.

The crystalline forms of hippuric and benzoic acids are shown in Figs. 101, 102, and 103.

The **Ammonium Salts** present in urine are an index to the neutralisation of acids in the body. Acid substances are produced in carnivora and omnivora as the result of metabolism—for example, carbonic, phosphoric, and sulphuric acids—and these would prove highly poisonous were it not that ammonia, which neutralises them, is simultaneously formed. This defensive mechanism against acidosis depends on smaller amounts of ammonia being converted into urea. When, as occurs in herbivora, there is already an excess of alkali in the diet, a sufficiency of bases is present to neutralise the acid formed during metabolism, so that the normal conversion of ammonia into urea continues. The evidence which bears on this is afforded by the injection of acids into the circulation. This, in a dog, does not alter the reaction of the blood, for ammonia is produced in sufficient quantities to neutralise the acid. In herbivora, on the other hand, the ready supply of ammonia may not be available; the store of vegetable alkaline salts is soon used up, for we have already seen the heavy draft on these which hippuric acid alone makes, so that the animal as the result of the injection of acid suffers more acutely and is more readily killed by acidosis than is the case with carnivora. Doubt, however, has been thrown on this difference between carnivora and herbivora in the matter of acidosis, and Armsby draws attention to the fact that if the amount of protein in the diet is low, as it frequently is, there is relatively less ammonia available than is the case with carnivorous animals.

It is rather a difficult matter to increase the acidity of an acid urine. Mineral acids effect it, but if the acid be pushed too far ammonia is split off from the protein in order to prevent toxic results. On the other hand, it is very easy to increase the alkalinity of an alkaline urine. It may be well to explain that the poisoning which occurs from acidosis is due to the reduced carrying power of the blood for carbon dioxide. In consequence, this substance is retained in the tissues with fatal results. The administration of ammonium carbonate by the mouth will not prevent this condition, since it appears in the urine as urea.

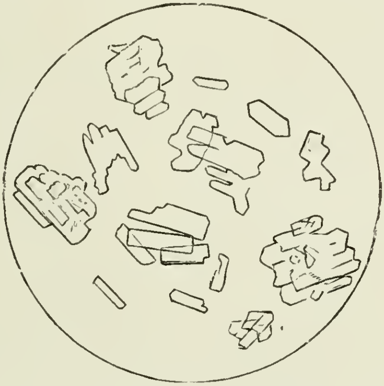

FIG. 103.—CRYSTALS OF BENZOIC ACID.

Free ammonia exists in the urine of the horse. It may be owing to ammoniacal fermentation in the bladder, but it is quite certain that perfectly fresh urine may give marked evidence of the presence of free ammonia. On standing a short time outside the body, especially in summer weather, the urea decomposes, as previously mentioned, and ammonium carbonate is largely formed. Recent work by Beccari in Italy confirms the presence of free ammonia in the urine, not only of horses, but of cattle.

Sulphuric Acid.—The sulphates in the urine, especially in that of herbivora, and more particularly in the urine of the horse, are an excretion of considerable importance. In all animals three varieties of sulphur-containing substances are found—viz.:

Inorganic sulphates.
Neutral sulphur.
Ethereal sulphates.

From this it might be supposed that the sulphates taken into the body with the food are considerable. As a matter of fact, the sulphates in food exist only in traces, and most of the sulphur-containing substances in urine are really derived from the oxidation of the amino-acid, *cystine*, which contains the organic sulphur of protein.

The *Inorganic Sulphates* are believed to be derived from the katabolism of proteins in the intestinal canal, or, at any rate, from the destruction of protein substances not yet forming part of the body; hence they are spoken of as the exogenous portion. The quantity of sulphates excreted in this form varies considerably, as it depends upon the amount of protein in the diet. They pass from the body as salts of sodium and potassium.

The *Neutral Sulphur* is furnished from the actual proteins of the tissues; it is not liable to great variations in quantity, and the amount for the individual may even be constant. Included with it is the sulphur of the pigment urochrome, cystine, thiocyanates, and minor sulphur compounds, such as ethyl sulphide, found in the urine of the dog, and sulphocyanic acid said to be a constant constituent of the urine of herbivora.

Coming between the above is a third variety of sulphur compounds—the *Ethereal Sulphates*, which are furnished by the tissue proteins, but also by non-protein substances; they are a very characteristic group in the urine of the herbivora, especially in that of the horse. The sulphur forms compounds with such poisonous substances as indol, phenol, skatol, kresol; these are produced in the intestinal canal of the animal in consequence of the disintegration of protein substances, but also from certain aromatic constituents in vegetable food. These bodies are either excreted unabsorbed from the intestinal canal, or if absorbed, unite in the blood-stream with an alkaline sulphate to form conjugated or ethereal sulphates, and in this way are rendered innocuous.

The compounds formed by sulphuric acid with the aromatic bodies are potassium phenyl, kresyl, indoxyl, and skatoxyl sulphates.

To the compound potassium indoxyl sulphate the name *indican* has been given. This substance on oxidation yields indigo blue, and is comparatively abundant in the urine of the horse. Phenyl-sulphuric acid in the presence of air undergoes oxidation, and yields *pyrocatechin*, which gives the brown colour to the stale urine of the horse. In the dog, glycuronic acid may be united to some of the skatol and phenol, and this substance exercises a reducing action on salts of copper, which might be mistaken for the action of dextrose.

In man and the dog the ethereal sulphates are regarded as a measure of protein disintegration, but in the horse this is not so, for we have already seen that ethereal sulphates in this animal may be derived from aromatic constituents in vegetable food.

Cystine, which, as we have seen, is the chief source of sulphur in the body, is readily oxidised to sulphuric acid, and the neutralisation of this is another source of drain on the bases of the body. Where the protein in a diet is in excess, as, for instance, in the case of a horse fed wholly on oats, the amount of acid, both sulphuric and phosphoric, is in excess of the available bases, and the urine becomes acid. A pound of protein may contain sufficient sulphur to yield on complete oxidation an ounce by weight of concentrated sulphuric acid. In a properly balanced diet the herbivora obtain a surplus of bases which more than neutralise the acid salts contained in concentrated foods.

Non-Nitrogenous Organic Substances.—The amount of these in the urine of herbivora is relatively considerable (Armsby). Their origin is imperfectly known, excepting that they are derived from the food, especially those constituents described in analyses as ‘ crude fibre,’ ‘ bodies related to carbohydrates,’ and ‘ nitrogen free extract.’ These substances do not undergo complete oxidation to carbon dioxide and water, and in consequence are excreted in the urine as imperfectly oxidised substances. As might be expected, a diet of hay or straw causes a larger excretion of these substances, but precisely how they originate is unknown.

The **colouring matter** of the urine is a question not fully settled. There are known to be several pigments, the chief one being *urochrome*, which is probably an oxidation product of *urobilin*. Urobilin is formed from stercobilin, which is absorbed from the intestinal canal. The mother-substance of urobilin is a *chromogen*, which yields urobilin on oxidation.

The **Inorganic Substances** found in the urine are calcium, magnesium, sodium, and potassium, existing in the form of chlorides, sulphates, phosphates, and carbonates. The origin of these salts is, first, the food taken into the body; secondly, the metabolic processes occurring in the tissues. The nature and amount of the salts varies with the class of animal and the character of the food. In the urine of the horse calcium and potassium salts predominate, sodium and magnesium are present in small amounts, phosphates are practically absent, while sulphates and chlorides are in considerable quantity. It has been found that in ruminants the calcium salts are mostly excreted with the fæces, whereas in the horse they principally pass through the kidneys. It is certain that phosphates, so important a feature in the urine of carnivora and omnivora, are in the horse almost wholly excreted by the intestines.

Calcium.—More lime exists in the urine of the horse than is soluble in an alkaline fluid, so that it is found both in suspension and in solution; the amount of the former increases with the age of the urine, owing to the development of ammonia, until nearly the whole of the lime is precipitated. The lime exists in combination with oxalic, carbonic, hippuric, and sulphuric acids; all these combinations do not necessarily exist in one specimen of urine, the salts formed depending on the varying relative amounts of the acids formed in metabolism. The amount of lime in the food does not influence the elimination through the kidneys; more lime, however, is found in the urine of horses at work than in that of those at rest. Oxalate and carbonate of lime crystals are common microscopic deposits in the urine of the horse (Figs. 104 and 105). The oxalic acid is derived from the oxalates contained in the vegetable substances of the food.

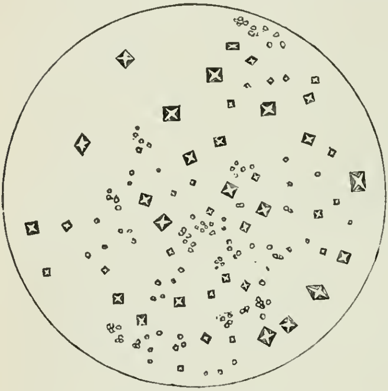

FIG. 104.—CRYSTALS OF OXALATE OF LIME (FUNKE).

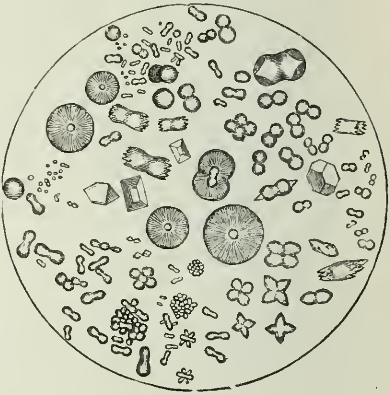

FIG. 105.—CRYSTALS OF CARBONATE OF LIME (FUNKE).

The turbidity of the healthy urine of the horse is due to suspended calcium carbonate. This may be proved by the addition of an acid, which causes profuse evolution of gas, when a clear, transparent urine results. Simple as the point is to understand, it would appear that in practice turbid urines in the horse are regarded as pathological, and that the marked deposit which follows every evacuation of urine is considered incompatible with a normal condition. The fact is, that no healthy horse passes anything but a turbid urine, sometimes with a considerable deposit, but always with a deposit. This may be seen in the stable, or in the road, after the urine has either soaked in or partly dried, as a fine, yellow, sandy-looking deposit. The 'sand' is calcium carbonate; the yellow colour is the pigment of the urine. It is most remarkable that vesical calculus in the horse is so rare, considering the fact that from the pelvis of the kidney onward the urine has far more mineral matter in it than it can hold in solution; fortunately it rarely coheres.

Magnesium.—There is but little magnesium in the urine of the herbivora, its chief excretory path being the bowels. The sheep is an exception to the general rule that in the urine magnesium is excreted in smaller amounts than calcium. Magnesium exists in the urine partly in solution and partly in suspension, the latter being principally due to ammoniacal fermentation.

Potassium, derived from the potash of the food, exists largely in the urine of herbivora; it forms numerous combinations, the one with carbonic acid being the cause of the fixed alkalinity of the urine in the horse. There is more potash found in the urine of horses at rest than in that of those at work; this is explained by the considerable amount of potassium excreted with the sweat. *Sodium* exists in the urine of herbivora only in relatively small quantities, on account of the fact that very little sodium is found in vegetable food. For the relationship between potassium and sodium in the body, see p. 382.

Chlorine is supplied by the chlorides of the food. The proportion of chlorides in the food of herbivora is not very high; the amount excreted by horses, combined with sodium, was found by us to equal a daily excretion of 5·5 grammes (85¼ grains) of common salt. Salkowski places it much higher—viz., about 27 grammes (¾ ounce) daily.

Phosphoric Acid, though existing in large quantities in food such as oats, passes off almost wholly by the alimentary canal. Sometimes only traces are to be found in the urine of herbivora; at others the amount is appreciable, but never considerable. Work does not influence its production. In the urine of carnivora the phosphates are an important constituent. They exist in the urine in two forms—viz., alkaline phosphates, such as phosphate of sodium or potassium, and earthy phosphates, such as phosphates of calcium and magnesium; these triple phosphates are common as a microscopical object in the decomposing urine of the horse, though trifling in actual amount (Fig. 106). The phosphates are derived from the food and tissues. According to Munk, if there is an abundance of lime salts in the diet, as in vegetable food, the phosphates are not eliminated to any extent by the kidneys, for the reason that they combine in the intestinal canal with lime and magnesia, and pass off by that channel; if, on the other hand, there is but little lime and magnesia in the intestines, the phosphates are united to soda and potash, pass into the blood, and are eliminated by the urine. In febrile conditions in the herbivora phosphates appear in the urine in marked amounts.

The **Reaction** of the urine in carnivora is acid, due to acid sodium phosphate; in omnivora the reaction is acid or alkaline, depending upon the nature of the diet, an animal diet producing an acid, a vegetable diet an alkaline, urine. In herbivora the reaction is alkaline in health and under a suitable system of diet. Where protein is supplied in excessive amounts, especially in the absence of hay, the urine becomes acid. Vegetable food may result in acid or alkaline salts predominating in the urine. All the cereals, with the exception of bran, possess an excess of acid salts; all grasses, hay, straw, and roots possess an excess of alkaline salts. It is the excess of acid salts in oats which causes the urine of the horse to possess an acid reaction when fed on this grain without hay. Acid salts are also formed from fermentable material, such as grass and silage; most of these acids are neutralised, though others, such as tartaric, malic, and oxalic, are oxidised with difficulty. The organic acids appear in the urine as carbonates in combination with lime and potash. The greater part of the alkalinity of the urine in the horse is due to carbonates of potash and lime; there is a further alkalinity outside the body, the result of the development of ammonia.

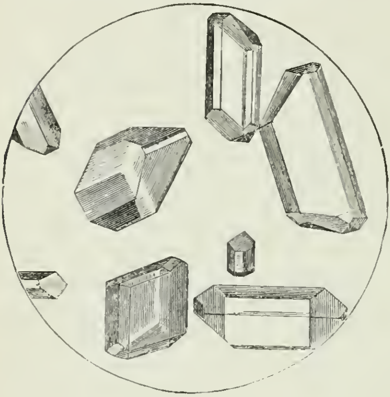

Fig. 106.—Crystals of Triple Phosphate (Funke).

No free acid exists in the urine of any animal.

The **amount of water secreted** with the urine differs considerably in the various classes of animals. It is generally considered that in the horse, of the total intake of water, not more than one-third leaves the body by the kidneys. The writer obtained, as the mean of many observations, 4·8 litres (8½ pints) of urine in twenty-four hours. This agrees with the observations of Munk,* who regarded 3 to 4 litres as the mean excretion in the horse. In the ox a larger amount of urine is passed—6 or 10 to

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* Quoted by McKendrick.

25 litres (10, 17, 44 pints) daily; in sheep, 0·3 to 0·9 litre (½ pint to 1½ pints); pigs, 1·5 to 8 litres (2·6 to 14 pints); dogs, 0·5 to 1 litre (0·8 pint to 1·6 pints). Tereg,* who gives this table, states that the excretion of water by the kidneys and other channels in the various classes of animals is as follows:

> Herbivora: 20 per cent. excreted by the urine; 80 per cent. by lungs, skin, and bowels.
>
> Omnivora: 60 per cent. excreted by the urine; 40 per cent. by lungs, skin, and bowels.
>
> Carnivora: 85 per cent. excreted by the urine; 15 per cent. by lungs, skin, and bowels.

Food rich in nitrogen causes a greater secretion of urine.

Horses at work excrete less urine than those at rest, no doubt owing to the loss by the skin. In winter, in consequence of the lessened action of the skin, more urine is excreted than during summer. Lieut.-Colonel Head, C.M.G., R.A.V.C., noted the amount of urinary excretion in horses affected with mange, before and after dressing the body with an oily application. He found that those undressed furnished from 8 to 10 pints of urine a day, but after dressing the amount secreted rose to 14 or even 18 pints. On washing off the dressing the quantity of urine returned to normal. (*Communicated.*)

The Urine of the Horse.

Specific Gravity.—This varies within wide limits dependently on the diet and the amount of dilution. The mean of a large number of observations was 1·036, the highest registered was 1·050, and the lowest 1·014.

The *Quantity* of urine is liable to very considerable variation, depending on the season and the diet; the more nitrogen the food contains the larger the amount of water consumed, and the greater the bulk of urine excreted. The mean of many observations was 4·8 litres (8½ pints) in twenty-four hours, the diet being moderately nitrogenous, but in individual instances very much more than this may be obtained—viz., 6 to 11 litres (12, 15, or even 20 pints).

The *Odour* of urine is said to be due to certain aromatic substances of the phenol group. Perfectly fresh urine has commonly a most distinct, though faint, smell of ammonia. This may be due to fermentative changes occurring in the urea before the urine is evacuated. The normal fluid is always turbid, some specimens more so than others; very rarely is it clear, and then only for a short time. The turbidity is due to the amount of suspended carbonates of lime and magnesia; on standing, particularly if it is undergoing ammoniacal fermentation, the turbidity becomes intense.

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* Ellenberger, *op. cit.*

The *Consistence* of the fluid depends upon sex, and perhaps on the season. It is certain that some mares excrete a glairy, tenacious fluid which, owing to the amount of mucin it contains, can be drawn out in strings. It is very common to find the urine as thick as linseed oil, and very rare to find it fluid and watery. During œstrum the urine is of the consistence of oil. On a diet of oats and no hay, the urine may be so mucinous as to pour like white of egg. The mucin of horse's urine is a glucoprotein, containing 12 per cent. nitrogen and nearly 2 per cent. sulphur. The carbohydrate radicle, calculated as glucosamine, amounts to 30 per cent. (A. V. Sahlstedt.)

The *Colour* of fresh urine is yellow or yellowish-red, due to the pigment *urochrome.* On standing, the fluid rapidly turns brown, the dark tint commencing on the surface, and gradually travelling into its depth. The cause of the colour on standing is due to the oxidation of pyrocatechin (see p. 345).

The *Total Solids* consist of organic and inorganic matter, of which, on a mixed diet, 142 grammes (5 ounces) are organic, and 83 grammes (3 ounces) inorganic; these quantities are liable to great variation, sometimes being found greatly in excess of those quoted. The total solids are considerably affected by the diet; E. Wolff* found that, when he reduced the hay and increased the corn ration, the solids in the urine decreased, whereas on a diet consisting principally of hay and but little corn the solids increased; for example—

> On a diet of 8 kilogrammes of hay and 2 kilogrammes of oats there were 566 grammes of total solids.
>
> On a diet of 4 kilogrammes of hay and 6 kilogrammes of oats there were 460 grammes of total solids.

The percentage composition of the mineral solids is given in the following table by Wolff, the diet being hay, oats, and straw:

Potassium	36·85 per cent.
Sodium	3·71 ,,
Calcium	21·92 ,,
Magnesium	4·41 ,,
Phosphoric acid	—
Sulphuric acid	17·16 ,,
Chlorine	15·36 ,,
Silicic acid	0·32 ,,

In the table on p. 352 are given the results obtained by the writer in examination of the twenty-four hours' urine of horses at rest and at work.†

Salkowski‡ examined the urine of the horse, and gives the following as the composition of one specimen:

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* Ellenberger.

† 'Chemistry of the Urine of the Horse,' Proceedings of the Royal Society, vol. xlvi., 1889.

‡ Ellenberger's 'Physiologie.'

Water	1·8 litres	3·50 pints.
Organic solids	198·0 grammes	6·25 ounces.
Ash	50·0 ,,	1·60 ,,
Urea	92·0 ,,	3·25 ,,
Ammonia	0·357 gramme	5·53 grains.
Hippuric acid	15·60 grammes	0·49 ounce.
Phenol	2·44 ,,	37·89 grains.
Organic sulphur	13·46 ,,	208·69 ,,
Inorganic sulphur	5·33 ,,	85·77 ,,
Phosphoric acid	0·22 gramme	3·40 ,,
Lime	5·70 grammes	88·50 ,,
Sodium chloride	27·12 ,,	0·87 ounce.

In the following summary of the urine of animals other than the horse, the main facts are those given by Tereg.*

The Urine of the Ox.

The urine of the ox is much the same as that of the horse, excepting that it is secreted in larger quantities, 5·7 to 22·8 litres (10 to 40 pints) per diem. The fluid is clear, yellowish, and of an aromatic odour; it is of a lower specific gravity than that of the horse, 1·020 to 1·030 (in milch cows, according to Munk, 1·006 to 1·015), owing to the larger amount of water secreted. The nitrogenous matter found in the urine is represented mainly by urea and hippuric acid; in contrast to the urine of the horse, hippuric acid is always present. On a diet of wheat straw, clover hay, beans, starch, and oil, the amount of urea may be 4 per cent., while on one of oat straw and beans, it may fall to less than 1 per cent. When the percentage of urea is high, that of the hippuric acid is low, and *vice versa*. The largest amount of hippuric acid is produced by feeding on the straw of cereals, the smallest is furnished by feeding on leguminous straw, whilst a medium amount is produced by feeding on hay. It was stated many years ago by Faas that the urine of the working ox is turbid, and contains so much hippuric acid that a pound of this substance could be obtained by precipitation with hydrochloric acid. The amount of urine from which it was extracted is not given. The urine of ruminants contains less aromatic sulphur compounds than that of the horse, and more inorganic sulphur; as in the horse, the phosphates are either absent or occur only in small amounts.

On a diet of 8·45 kilogrammes of meadow hay, the urine had the following composition:

Quantity	7·57 kilogrammes.
Specific gravity	1·042
Hippuric acid	98·0 grammes.
Urea	131·0 ,,
Ash	350·0 ,,

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* Ellenberger's 'Physiologie.'

COMPOSITION OF URINE OF HORSE.

	At Rest		At Work.	
Quantity	5·0 litres	8·69 pints	4·5 litres	7·88 pints
Specific gravity	—	1·036	—	1·036
Total solids	230·0 grammes	8·11 ounces	232·0 grammes	8·19 ounces
Organic solids	146·0 ,,	5·15 ,,	152·0 ,,	5·37 ,,
Inorganic solids	83·0 ,,	2·94 ,,	80·0 ,,	2·82 ,,
Urea	98·4 ,,	3·47 ,,	98·4 ,,	3·47 ounces
Ammonium carbonate as urea	13·0 ,,	0·46 ounce	13·0 ,,	0·46 ounce
Ammonia	2·5 ,,	0·09 ,,	5·4 grammes	0·19 ,,
Benzoic acid	6·5 ,,	0·23 ,,	—	—
Hippuric acid	—	—	15·6 grammes	0·55 ,,
Phosphoric anhydride	1·13 grammes	0·04 ,,	1·7 ,,	0·06 ,,
Sulphuric anhydride	10·5 ,,	0·37 ,,	15·3 ,,	0·54 ,,
Other sulphur compounds	7·37 ,,	0·26 ,,	7·6 ,,	0·27 ,,
Chlorine	31·7 ,,	1·12 ounces	21·8 ,,	0·77 ,,
Calcium oxide	3·4 ,,	0·12 ounce	1·7 ,,	0·06 ,,
Magnesium oxide	2·8 ,,	0·10 ,,	2·5 ,,	0·09 ,,
Potassium oxide	33·7 ,,	1·29 ounces	27·0 ,,	0·95 ,,
Sodium oxide	2·5 ,,	0·09 ounce	1·7 ,,	0·06 ,,

Calves still suckling excrete an acid urine containing uric acid, allantoine, and creatinine. It is poor in urea, and, according to Moeller, contains hardly 1 per cent. of solids.

The Urine of the Sheep.

This has an alkaline reaction, a specific gravity of 1·006 to 1·015, and the amount excreted in twenty-four hours varies from 0·3 to 0·9 litre (0·5 pint to 1·5 pints). Tereg gives the following percentage composition of a sample:

Water	86·48
Organic matter	7·96
Inorganic matter	5·56

The organic matter contained—

Urea	2·21
Hippuric acid	3·24
Ammonia	0·02
Other organic substances	2·07
Carbonic acid	0·42
	7·96

The inorganic matter contained—

Chlorine	1·05
Potassium chloride	1·84
Potassium	2·08
Calcium	0·07
Magnesium	0·20
Phosphoric acid	0·01
Sulphuric acid	0·24
Silica	0·07
	5·56

It will be observed from the table how rich the urine of the sheep is in hippuric acid. In the urine of sheep there is very much more magnesia than lime, consequently the reverse obtains in the fæces of this animal.

The Urine of the Pig.

This resembles that of carnivora, but its composition depends on the character of the food. The specific gravity is 1·003 to 1·025. It is either acid or alkaline; it contains uric acid, hippuric acid, xanthine, guanine, and much urea; the amount excreted varies between 1·5 to 8 litres (2½ to 14 pints).

In the following analysis of the urine the diet consisted of peas, potatoes, and sour milk:

Total urine	4·1 kilogrammes (7 pints).
Specific gravity	1·018
Dry substance	2·768 per cent.
Total nitrogen	0·604 ,,
Ammonia	0·024 ,,
Ash	1·234 ,,

The ash consists largely of phosphates and potassium salts, a moderate amount of magnesium, and very little sodium or calcium.

The Urine of the Dog.

It is impossible to give the composition of the urine of the dog, as the amounts of constituents secreted vary considerably according to the nature of the diet.

The urine is acid in reaction on a flesh diet, the acidity being due to acid phosphate of soda; on a vegetable diet it may be alkaline. The amount excreted is from 0·5 to 1 litre (¾ pint to 1¾ pints) daily, but varies with the size of the animal and the nature of the diet; the specific gravity is from 1·016 to 1·060, dependent on the diet; the colour is pale yellow to straw-yellow; the urea varies from 4 per cent. to 6 or 10 per cent. On an animal diet uric acid (allantoine; see p. 340) is excreted, but disappears on vegetable food being given. Certain breeds of dogs —Dalmatians—are stated to have a high uric acid elimination; hippuric acid in small quantities appears with fair regularity; sulpho-cyanic acid is present, especially after a diet rich in purins; indican and phosphoric acid are well-marked constituents. Glycuronic acid may be found; it is an oxidation product of glucose, and exists in traces, but after the administration of camphor or chloral it is obtained in well-marked quantities. It is a point of practical importance to avoid regarding a urine which reduces salts of copper as necessarily containing sugar, for glycuronic acid is a reducing substance. The presence of bilirubin in the urine of the dog has been noted by Salkowski.

As an illustration of the variation of the dog's urine, dependently on the nature of the diet, we may take an example from a long series of experiments by Bischoff and Voit.

On a diet consisting of meat 0·57 pound, starch 0·71 pound, salts 77·5 grains, a specimen of urine gave the following composition:

Amount - - -	252 c.c.	0·44 pint.
Specific gravity - -	—	1·049
Urea - - -	21·0 grammes	326·6 grains.
Salts - - -	5·53 ,,	85·6 ,,

On a diet consisting of meat 2·75 pounds and fat 0·55 pound, the following was the composition:

Amount - - -	702 c.c.	1·23 pints.
Specific gravity - -	—	1·054
Urea - - -	80·7 grammes	1,351 grains.
Salts - - -	12·21 ,,	189 ,,

The Discharge of Urine.—The urine is constantly being secreted, and it either trickles or is propelled by rhythmic muscular contractions down the ureters to the bladder. It is quite likely that both movements take place, depending upon the condition of bladder distension; whereas 'trickling' is suitable for an empty bladder, some muscular effort on the part of the ureters will be required when the bladder is full. Either drop by drop or by 'spirts' the urine enters the bladder, which gradually advances in the pelvis, and rises in the direction of the sacrum. All reflux of urine into the ureters is prevented by the oblique manner in which the coats of the bladder are pierced, so that the greater the internal pressure the tighter are the ureters closed. If circumstances prevent the evacuation of the bladder contents, the organ gradually advances to the brim of the pelvis, and then impinges on the abdominal cavity; in a state of extreme distension it may project for some distance into the cavity, the weight of the fluid having a tendency to cause the organ to incline towards the floor of the abdomen. In the chapter on the Muscular System attention will be directed to the fact that the muscle of the bladder may alter its length, so as to admit of increased distension of the organ without any increase in the tension of its walls (see p. 437).

The entrance to the urethra is controlled by a circular layer of unstriped muscle, part of the bladder muscle, but outside this is a band of voluntary muscle, which must be regarded as part of the urethra. Physiologists are not agreed as to the mechanism involved in the act of micturition. Ordinarily it is a voluntary act, but the dog, its spinal cord having been divided in the lumbar region, will carry out the process perfectly, though there can be no question of consciousness involved. In this case the afferent impulses conducted to the cord by the second and third sacral nerves stimulate a *vesical centre* in the grey matter of the sacral cord. There can be no doubt that, under ordinary circumstances, the act is a voluntary one. The efferent nerves supplying the bladder are derived from two sources—viz., directly from the sacral spinal nerves, and, secondly, through the sympathetic. The sacral nerves furnish the *nervus erigens*, which is connected with the hypogastric plexus, while the sympathetic supply is furnished by the second to the sixth lumbar ganglia; these pass to the inferior mesenteric ganglion, and issue from it as the hypogastric nerves. Stimulation of the *nervus erigens* causes relaxation of the sphincter and contraction of the wall of the bladder, while the hypogastric nerves, though relaxing the wall of the bladder, contract the sphincter. The latter action is antagonistic to that of the spinal nerve supply. It is almost certain that the most important supply to the bladder is the *nervus erigens*.

At the moment the bladder wall begins to contract, it is assisted by the abdominal muscles and a fixed diaphragm. The flow is never so powerful in the female as in the male, the final expulsion of the last drops from the urethra of the latter being effected by the rhythmical contraction of the perineal muscles and by the *accelerator urinæ*. During the act both the horse and mare stand with the hind-legs extended and apart, resting on the toes of both hind feet, thereby sinking the posterior part of the body. The male animal also often advances the fore-legs in order to avoid their being splashed; in this position the penis is protruded, and the tail raised and quivering. The streams which flow from the two sexes are very different in size, depending on the relative diameters of the urethral canal. The mare after urinating spasmodically erects the clitoris, the cause of which is difficult to see; it may be due to the passage of a hot alkaline fluid over a remarkably sensitive surface. The horse can, under ordinary circumstances, pass urine only when standing still, though both sexes can defæcate while trotting; but in a condition of œstrum the mare can empty her bladder while cantering. In the ox the urine simply dribbles away, owing to the curved character of the urethral canal, and is directed towards the ground by the tuft of hair found on the extremity of the sheath. The ox can pass his urine while walking. The cow arches her back to urinate, but instead of extending her hind-limbs, as does the mare, she brings them under her body, at the same time raising the tail.

The upright position is essential to micturition; no horse of either sex can evacuate the bladder while lying down—a point of extreme importance in practice.* Further, it will be remembered that the fundus of an over-distended bladder hangs into the abdominal cavity, and is thus on a lower level than the urethra; this contributes to the difficulty of emptying an over-distended organ. As a horse cannot micturate at work, it is obvious that opportunity for this should be regularly afforded, or much suffering must result.

Pathological.

There is scarcely any organ of the horse's body so free from disease as the kidneys. The material in the pelvis of that organ, which looks like pus, and is frequently so described, is really the natural mucus of the urine, mixed with insoluble lime salts. We have never found sugar in the horse's urine; it is, however, stated that sugar is present in the urine of animals after chloroform or ether anæsthesia. Protein is not uncommon, but only as the result of inflammatory affection of the lungs and pleura.

Vesical calculus would be one of the most common diseases of herbivora were it not that they excrete the insoluble salts at each evacuation of the bladder and that calcium carbonate, their invariable component, has but little tendency to cohere. Nevertheless, calculus of the kidney and bladder, and the so-called sabulous deposits in the bladder, are by no means unknown both in the horse and ox. In sheep the sabulous matter may obstruct the vermiform appendix of the penis. In the dog uric acid is the most common constituent of vesical calculus.

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* At the moment of violent death from destruction of the brain, the urine dribbles away while the horse is lying on its side.

CHAPTER XI

NUTRITION

THE nutrition of the domesticated animals, especially of those intended for food, has, owing to its economic bearing, been studied with the greatest care for many years past. There can be no doubt that far more is known of their nutrition than of that of man, the reason for which is obvious. Investigations of this character are extremely laborious, and require the united labours of the chemist, physiologist, and stock-feeder; in the first instance they were made with the object of ascertaining the nutrition of animals intended for the purpose of food, but in more recent years they have included inquiries into the nutrition of working animals. The subject is still far from exhausted; many problems await solution, especially those dealing with the chemical changes by which the elements of food are built up into the body, and later pulled down for its utilisation. In many cases only the beginning and the end of these processes are known with anything approaching exactitude, and it is probable that we shall never know how the dead food substances become living tissue.

Composition of the Body.—The animal body consists of proteins, fats, salts, and water, together with a small proportion of carbohydrates. The proteins are nitrogenous substances of extraordinary complexity and variety, and it is only within recent years that any light has been thrown on the nature of the basic substance, protein. Its molecular weight affords a good idea of its complexity. The molecular weight of egg albumin is given as 5,378, of the globin of hæmoglobin at 5,000 to 8,000, while that of the globulin, edestin, from hemp seed, has been stated to be 14,500. The feature which distinguishes the proteins is that they all contain nitrogen in addition to carbon, hydrogen, and oxygen. The fats contain carbon, hydrogen, and oxygen only; the carbohydrates, represented in the vegetable world by starch, sugar, etc., contain the same elements as fat, but in different proportions; the salts of the body are in all the tissues and secretions, and the water is everywhere. The water in the body predominates in respect of weight over the other constituents, the weight of the salts being the least, if the small and variable amount of carbohydrate be excluded. The proportion of fat is always greater than that of protein, though the condition of the animal decides what this amounts to.

The following table from Lawes and Gilbert shows the percentage proportions of these various tissues in oxen, sheep, and pigs in lean and fat condition. The figures given are those recalculated by Armsby* on the basis of 'empty weight'†—*i.e.*, the live weight minus the contents of the digestive canal.

	Oxen.		Sheep.		Pigs.	
	Half Fat.	Fat.	Lean.	Fat.	Fat.	Lean.
Water - -	56·1	48·4	61·0	46·2	58·1	43·0
Protein- -	18·4	15·4	15·8	13·0	14·6	11·4
Fat - -	20·8	32·0	19·9	37·8	24·6	43·9
Ash - -	5·0	4·2	3·4	3·0	2·8	1·7

Half of the water and half the protein found in the body are contained in the muscles, which represent about 45 or 50 per cent. of the body weight.

Income and Expenditure.—The *Income* of the body consists of carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, salts, and water. These are contained in the protein, fat, carbohydrate, and salts of the food; the oxygen is mainly supplied by the air taken in at the lungs.

The *Expenditure* of the body made up of the same elements, consists of what is removed by the lungs, urine, fæces, and skin. The *Nitrogen* is excreted almost wholly by the urine in the form of urea, hippuric acid, and other nitrogen-containing bodies. It is usual to regard the urinary nitrogen as a measure of the protein changes in the body, though it is obvious that the sweat, hair, and hoofs are also channels through which nitrogen is lost. The *Carbon* is excreted as carbonic acid by the lungs and in the various carbon compounds in the urine. The *Hydrogen* is removed as water by the lungs, skin, and urine, and in the herbivora a portion, as marsh and other gases, escapes by the respiratory passage and bowels. The *Salts* are excreted by the kidneys, skin, and glandular secretions. Among these channels of excretion we have not referred to the digestive tract. Broadly speaking, this may be regarded as being outside the body, and the material it contains as the unutilised residue which has formed no part of the system. This statement, however, is not strictly accurate, as there are excretions from the system into the digestive tract; especially is this true in the case of the salts.

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* 'The Nutrition of Farm Animals.' H. P. Armsby, Ph.D., LL.D., New York, 1917. To this excellent work I am greatly indebted in the preparation of this chapter. It contains an account of the classical experiments in animal nutrition, and of all recent advances.

† The empty weight in fat cattle is 91 per cent. of the live weight; in half-fat cattle, 89 per cent. to 90 per cent.; and in thin cattle, 87 per cent. to 89 per cent.

Tables have been prepared showing the income and expenditure of the body for both animals and man. They represent laborious experiments; everything passing into and out of the body has to be weighed and submitted to analysis to ascertain the nature and amount of the chemical elements concerned.

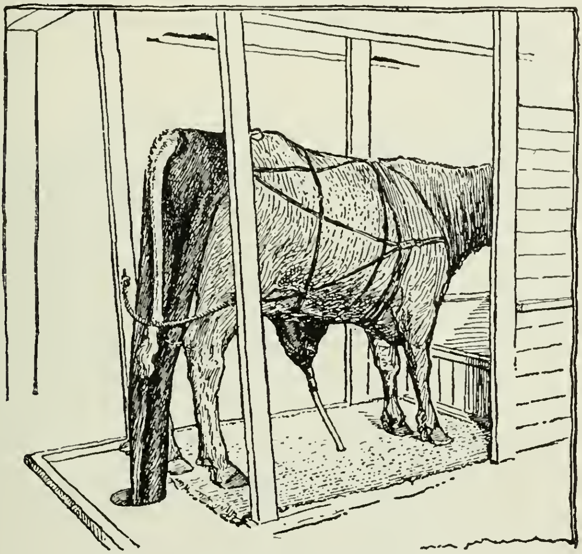

Fig. 107.—Steer in Digestion Stall (Bailey's 'Cyclopædia of American Agriculture').

The earliest method by which these data were arrived at was the simple one of collecting the urine and fæces of an animal living on a known diet, and determining the differences between the amounts of the elements in the food and in the excreta. This method was imperfect, for it neglected the excretions of the respiratory track and of the skin, but, nevertheless, it was a valuable means of inquiry, and is still employed in determining the digestibility of foods. The apparatus now used is shown in Fig. 107. In order to determine the income and expenditure by the respiratory passage, as well as the loss by the digestive canal and other sources, a *Respiration Chamber* is employed in which the animal under observation lives. Of these there are two types—in one the chamber is sealed, the consumed oxygen being replaced as required; in the other the chamber is open, the entering air being measured. In both types the gases produced are analysed and the constitution of them ascertained. The composition of the food is known, and the excreta are analysed in order to ascertain the chemical composition. In this way the amounts of the income and expenditure of the body are ascertained. There is probably no class of experiment so tedious as this. The work is continuous for twenty-four or forty-eight hours, and a very small error in the technique renders the whole observation useless. In the latest form of respiration chamber appliances have been introduced to enable a definite amount of work to be performed, and in this way the metabolism of the body at work as well as at rest, can be ascertained (see Fig. 108). The most advanced method of inquiry is by means of the *Respiration Calorimeter*, in which not only the above facts can be ascertained, but also the heat given out by the body and the use the body makes of the material supplied as food. Such an appliance for large animals has been erected at the Institute of Animal Nutrition of the Pennsylvania State College (see Figs. 109, 110). It is extremely costly, and so elaborate that it takes seven men to work it, exclusive of those in attendance on the animal.

Metabolism.—By this term are understood the changes occurring in living tissues. It is evident, from what has been said, that constant breaking down and building up is taking place in the body. Every muscular contraction, every respiration, the beating of the heart, and the movements of the bowels, all mean wear and tear, and as a part is destroyed it must be replaced. The process of construction is known as **anabolism,** and of destruction as **katabolism.** In a perfect state of health these should be in equilibrium. Both repair and destruction are dependent upon definite chemical changes occurring in the system, of some of which we have a fair knowledge, while others are obscure.

The metabolism of the tissues is apparently under the influence of the nervous system. We have previously studied a good example of this in the secretory nerves of the submaxillary gland, and it is probable, though our information on the point is very defective, that the nutrition of the body is largely directed by the nervous system. In some forms of lameness and injury in the horse we constantly observe muscular wasting, which is out of all proportion to the atrophy a part suffers by being simply thrown out of use, and which can only be explained by

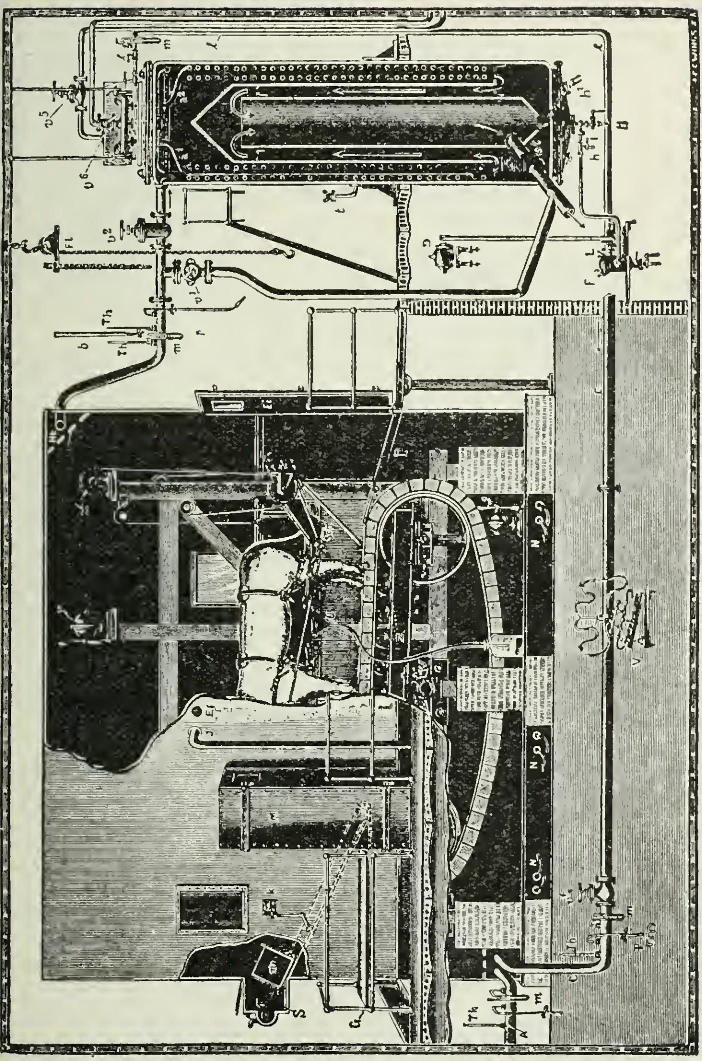

FIG. 108.—A REGNAULT-REISET RESPIRATION APPARATUS EMPLOYED BY ZUNTZ, FOR LARGE ANIMALS, SEEN IN SECTION (*Landw. Jahrbücher*, Vol. XLIV., Plate II.).

The animal stands on a movable platform, which, in the case of horses, may be made to revolve horizontally or at an angle, in order to study metabolism during work.

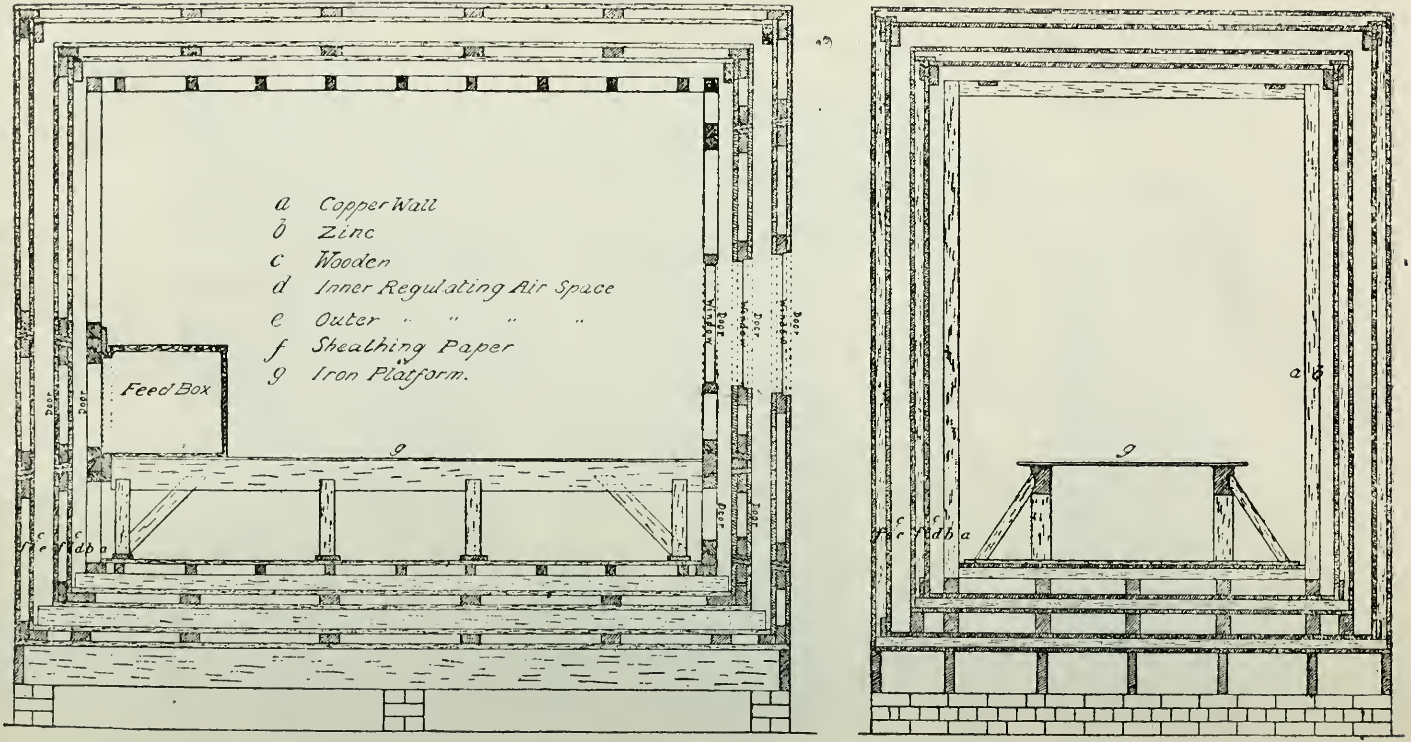
a Copper Wall
b Zinc
c Wooden
d Inner Regulating Air Space
e Outer " " "
f Sheathing Paper
g Iron Platform.
Feed Box
Door
Window
g
f e c f d b a
a b

Fig. 109.—The Atwater-Rosa Respiration Calorimeter for Animals: Vertical Cross Sections.

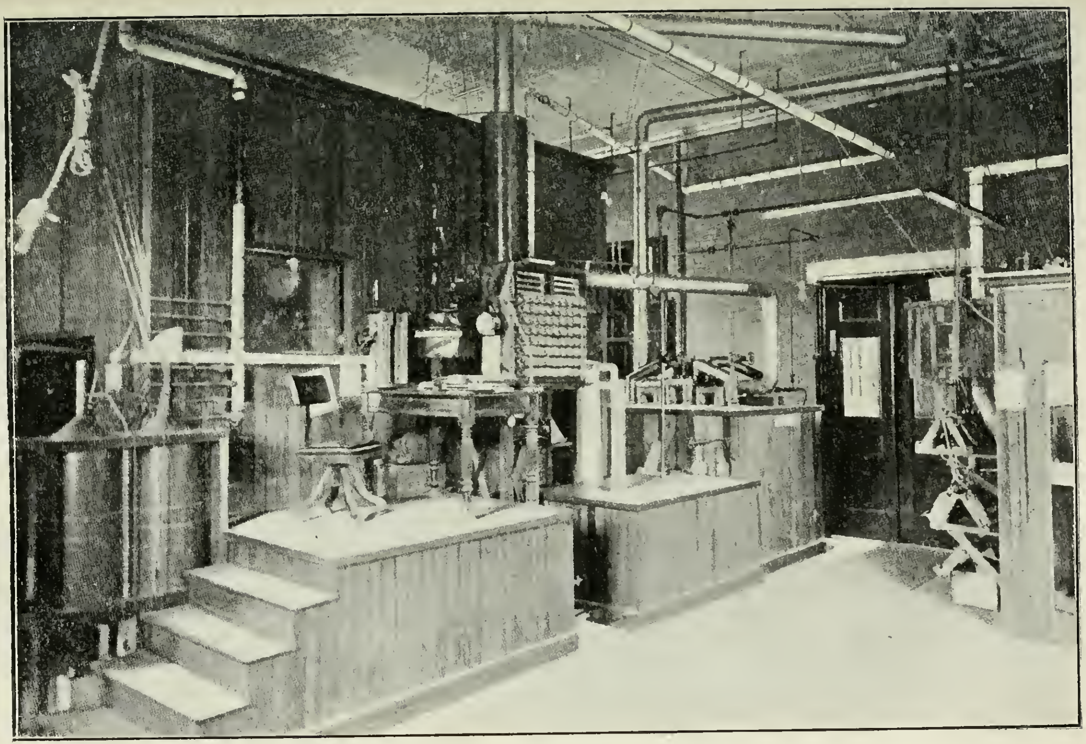

FIG. 110.—THE PENNSYLVANIA RESPIRATORY CALORIMETER FOR ANIMALS ARRANGED FOR EXPERIMENT. The chamber is on the other side of the glass window, to the left of the observer's chair.

injury to the trophic nerves which regulate the nutrition of the part. Even a better example is afforded by the peculiar changes which sometimes follow direct injury to trophic nerves, as in plantar neurectomy of the horse. The sloughing of the entire foot, or gelatinous degeneration of the phalanx, is due to injury of the trophic nerves. Injuries to the fifth pair of nerves have been followed by sloughing of the cornea, and pneumonia has followed division of the vagi, the sequelæ in both cases being possibly due to the loss of trophic influence.

Disordered nutrition of a tissue may show itself without any obvious injury to trophic nerves—as, for example, in the phenomenon known as inflammation, or in the well-known sympathy existing between the digestive system of the horse and the laminæ of the feet. Further evidence of nervous action is afforded by nutrition which is normal in character, such as the change of the coat with the season of the year. The influence of light on metabolism is also probably conveyed through the nervous system. In making these statements we must guard against the error of considering that no growth, repair, or reproduction can take place excepting under the influence of the nervous system. The trophic influence exercised by nerves appears to be directed to maintaining in equilibrium the processes of building up and breaking down which are occurring in all tissues. Though the metabolism of the body is largely regulated by the nervous system, yet the process cannot be carried out without food; metabolism goes on during starvation, for even then food is being supplied, inasmuch as the animal is living on its own tissues. The influence of light on metabolism, alluded to above, is well known in the fattening of cattle. The explanation is that more carbon dioxide is produced in the light than in darkness, and this indicates increased metabolism. By reducing metabolism fat is stored up. Dark stables for horses favour the putting on of fat, which is the antithesis of physical fitness.

Food must contain the substances required by the body—viz., water, protein, fat (or carbohydrate), and salts in the carnivora, and the same principles together with carbohydrate in the herbivora. In both cases an essential constituent of a normal diet are the *Vitamines*. Each of these proximate principles must be in a proper proportion, neither below nor in excess of the animal's requirements. Each must be present; nothing can replace protein nor salts; a carbohydrate-free diet in the herbivora would be fatal; a water-free diet in all animals sustains life for a shorter period than does water when there is an entire absence of food; and no diet, no matter how nutritious or digestible, sustains life if *vitamines* be absent. We have, therefore, to inquire why it is each of these substances is essential in every diet, and how each behaves in the system.

Nitrogenous Equilibrium.—The storing up of protein is an expression which has repeatedly occurred in the previous chapters and the impression may have been created that of the total protein in a diet some is daily stored up, so that less leaves the body than entered it. There can be no doubt that some of the protein of the daily diet is stored up, but the greater part is not. There is no more familiar fact than that the body may continue from month to month at much the same weight, and that could never be the case if storing up occurred daily. What occurs is this, that whatever total amount of nitrogen is received daily in the food, a similar amount is recovered daily from the excreta. Whatever portion of the protein of the food is converted into tissue protein, an equivalent amount of the latter is displaced, and appears in the urine as urea, hippuric acid, and other nitrogenous products; thus the total excretion of nitrogen equals the total receipts. A body in this condition is in nitrogenous equilibrium. It does not follow from this that it is not increasing in weight; it may be, owing to excess of non-nitrogenous food; on the contrary, it may be losing weight, due to a deficiency of non-nitrogenous material. The matter is of no moment at present, the main point being that in the urine an amount of nitrogen is excreted equivalent to that absorbed into the system from the food, and that such an animal is in nitrogenous equilibrium.

It is obvious that nitrogenous equilibrium cannot exist in young growing animals, nor in those in impoverished condition. In both these cases nitrogen is being stored up, as the tissue requirements are considerable, and therefore under these circumstances any attempt to establish nitrogenous equilibrium experimentally would fail. On the other hand, an adult animal in good condition gives off daily by the excreta as much nitrogen as it receives in the diet. If the ingoing nitrogen is increased, the outcoming nitrogen is increased; if the ingoing nitrogen is decreased, the outcoming nitrogen is decreased, and this is true within physiological limits.

It is evident, therefore, that in the same animal there may be different levels of nitrogenous equilibrium, and that these are dependent entirely on the income. The more the body receives, the more it spends; the less it receives, the less it spends, the important point being that the system is determined to make its expenditure of nitrogen equal its income. This being the case, how does the body behave when it receives no nitrogen? The previously improvident expenditure of nitrogen is now rectified. None is being received by the mouth, and the store in the tissues is therefore most economically expended.

If an animal experimentally subjected to fasting has previously been living on a rich nitrogenous diet, the fall in nitrogen excretion is not at first very obvious, but when this excess has been eliminated the output of nitrogen suddenly falls and remains at a minimum, there being a temporary rise as death approaches. During this experiment the animal has not been living entirely on its own protein tissues, but at first on the carbohydrate, which is rapidly exhausted, and then on the fat stored up. When the fat has been exhausted a heavier draft is made on the protein, which explains the temporary rise in the nitrogen output before death occurs.

The minimum nitrogen excreted during fasting is regarded as that which is essential to maintain the vital processes of the body, such as respiration, circulation, digestion, and, in the case of horses, the effort of standing.

A starving animal may be kept alive a longer time by being given some carbohydrate and fat. It will die because it is not receiving nitrogen, but the mixed carbohydrate and fat will effect economies in the store of body protein, and cause it to last longer. In this respect the carbohydrate is of much more value than the fat.

It was reasonable to suppose, as Liebig did, that the protein substances of the food, described by him as 'flesh formers,' carried out the mechanical work of the body. We now know better, for we have learned from the facts connected with nitrogenous equilibrium that the body continues to work satisfactorily though the equilibrium is established at different levels. Nevertheless, nitrogenous equilibrium, which we have seen possesses characteristic peculiarities, is affected by excessive work in man and animals, though it is correct to say that within normal limits it is unaffected by work.

The views laid down by Liebig were never seriously disputed until Lawes and Gilbert had completed their classical work, extending over twenty years, on animal nutrition at Rothamstead. During the years 1849-1859 these observers gave their results to the world, but it was a long time before their views were accepted. Though working at the question of the fattening of animals, and not at the question of energy, they were the first to announce that the value of a food for feeding purposes should not be calculated on the basis of the so-called flesh-forming' substances it contained, but of the non-nitrogenous elements.

We can now understand why it is that nitrogenous equilibrium experimentally established is produced on a smaller amount of protein when non-protein substances enter into the diet. No animals, not even the carnivora, live entirely on protein. The effect of the non-protein portion is to reduce the amount of protein destroyed, and to establish equilibrium at a lower level. Fat, starch, and sugar are protein economisers, while, conversely, a large protein diet is a fat obliterator, and this fact was turned to account by Banting in his treatment of obesity.

If a fasting animal be brought on to a protein diet equivalent to the amount of nitrogen being daily excreted, it would be reasonable to suppose that nitrogenous equilibrium would at once be established. Experimental inquiry shows this is not so, but that the effect of giving more nitrogen is to cause a greater excretion of this substance. It is not, in fact, until an amount of protein is given equivalent to at least three times the daily excretion during fasting that equilibrium is established. The explanation of this will now be given.

The Non-Nitrogenous Residue.—When the whole of the nitrogen has been split off from protein in the manner above described, there remains a residue which is formed in the following manner:

	Carbon.	Hydrogen.	Oxygen.	Nitrogen.
100 grammes protein contain - - - - -	53·00	7·00	24·00	16
34·29 grammes urea (from 100 grammes protein) contain - - -	6·86	2·29	9·14	16
Difference - -	46·14	4·71	14·86	—

This residue contains more than half of the hydrogen and oxygen of the protein, and the greater part of the carbon which has not been employed in the building up of urea, and it is from this portion of the protein molecule that glycogen, and perhaps fat, may be formed in the body. This explains the difficulty in obtaining nitrogenous equilibrium on a purely protein diet, and why more and more protein is required for the purpose. The animal is living on the non-nitrogenous residue, and the reason why it goes on consuming more and more protein is in order to obtain the necessary amount of carbon. This fact explains the extravagant nature of purely protein diets. It enables us to understand the loss in body weight which may be occurring even when nitrogenous equilibrium has been established, and to grasp a fundamental fact in feeding, that carbohydrate or fat added to such a diet enables equilibrium to be established on a lower plane in consequence of the economical effect it exercises on protein. The economising effect of fat or carbohydrate on protein is one of the well-established facts in dietetics.

Protein is not a single chemical substance, but a compound of several amino-acids, each of which has its function in the body. Gelatin, on which an animal will die, is deficient in tyrosine and tryptophan; the zein of maize lacks lysine, glycine, and tryptophan, and maize is therefore worthless for growth or as a maintenance diet when employed alone; the gliadin of wheat lacks lysine, and while wheat can maintain life it cannot promote growth. Yet both maize and wheat are food substances of the highest value, for the reason that they contain several proteins, and not a single protein, the deficiencies in one being balanced by excess in another. Recent researches, however, show that the absence of certain vitamines may be of far more importance than the absence of particular amino-acids.

Nitrogenous substances other than protein exist in both animal and vegetable foods; in some as much as one-third or one-half of the total nitrogen is not protein; for example, the nitrogenous glucosides, alkaloids, amino-acids, amids, nitrates, and ammonium salts of plants are obviously not protein. It is believed that in ruminants these bodies can be utilised in the first stomach in nourishing the micro-organisms which act on carbohydrates, and which by so doing economise the true protein of the food. It has even been thought that the protein of the micro-organisms may be utilised by the system.

The Metabolism of Protein.—When describing the digestion of protein substances in the digestive canal, sufficient was said to indicate the big gaps which exist in our knowledge of this question. Still greater ignorance exists of the subject now to be considered—viz., the behaviour and disposal of the protein matters after they have entered the system through the portal vein. The protein substances, once in the blood, are utilised in the repair and restoration of the tissues, but a study of nitrogenous metabolism has shown that under ordinary circumstances the extent of this repair is probably not considerable, and it certainly has proved that whatever portion of the protein is so used must turn out a similar amount of degraded material from the tissues, or the outgo of nitrogen would be less than the income. What is the probable behaviour of protein in the body until the stage of urea is reached ?

Pflüger taught that the whole of the absorbed material must first be converted into protein before any destruction of it can occur; in other words, that there is no route to urea excepting through the disintegration of the living cell. Voit held that the protein, when absorbed, is divided into two portions—one, the smaller, repairs wear and tear in the body, and he spoke of it as *tissue protein ;* the other circulates with the blood and lymph, and bathes the body cells, but does not form part of them. This protein is destroyed by the tissues with the liberation of heat and the formation of nitrogenous end-products, which escape by the urine. This portion Voit described as the *circulating protein.*

No positive statements can be made regarding the fate of protein in the body, as only the beginning and end of the process are known with anything like exactitude, but it is not unlikely that the story is as follows: The complex protein molecule in the digestive canal is hydrolysed by the digestive ferments, and split up into the simple amino-acids of lower molecular weight than the protein from which they have been derived. These amino-acids, of which there may be a large number in each protein, are what have been described as the 'building stones' of the body. They represent the material to be used in the repair of the tissues, and they gain access to the blood through the vessels in the intestinal walls. Until recently it was thought that before they could enter the blood they had to be reconverted to protein by the epithelium of the intestine, as no amino-acids could be traced in the blood. Recent inquiry has shown that amino-acids can be found in the blood, so that we may assume the protein material reaches its destination in the form of amino-acids, or as a combination of amino-acids known as *peptids.* In the tissues the process of reconstruction begins; the amino-acids are now synthesised under the influence of tissue enzymes, and by a reverse process to that which took place in the digestive canal they pass from simple bodies to the complex compound known as protein. Be it an animal or vegetable protein thus synthesised, its original likeness is lost in the tissues, and it becomes an animal protein of the specific pattern required by the particular part of the body into which it is built. The part played by intracellular enzymes in the production of this synthesis is no doubt of capital importance. It is possible that, by a reversed action, such as some enzymes have been proved to possess, the intracellular enzyme which builds up the cell is the same which carries out its katabolism. Urea may have its origin either from the destroyed cell or from the material sent to repair it; the latter view is generally favoured. All of the absorbed amino-acids are not synthesised, some are deaminised without playing a part in protein building, the ammonia being converted into urea and the non-nitrogenous portion used for energy production.

The above refers to the changes undergone by the simple proteins in the body, but there is another group represented in both animal and vegetable tissues, known as the conjugated or *nucleo-proteins,* where, among the end-products of digestion, are *purin* and *pyrimidine bases, pentoses* and *phosphoric acid;* these pass into the blood. The interest lies in the bases; purin yields *uric acid,* or *allantoine,* depending on the species of animal (see p. 339), while the end-products of pyrimidine are unknown. Neither base is wholly katabolised, for a portion of each appears in the urine. Urea is likewise formed from nucleo-proteins, a portion of the molecule, the NH_2 group, being split off as ammonia, as previously described.

It is believed that the building up of body tissues containing nucleic acid does not necessarily take place from the nucleo-proteins of the food, for it has been found experimentally that if purin bases be administered they are excreted. Further, the nucleo-proteins of the body may be repaired in the entire absence of this substance from the food. Evidently, then, the body cell can produce nucleo-proteins by synthesis, and in connection with this subject it may be added that it has recently been discovered that amino-acids may be formed in the body experimentally from ketonic or hydroxy-acids and ammonium salts.

The fates of the sulphur of proteins and of phosphorus in the nucleo-proteins have yet to be traced, but are best considered in connection with the general question of the metabolism of the salts of the body.

The proteins are most expensive food-stuffs, and dietary economists have repeatedly drawn attention to the unnecessarily nitrogenous, and therefore wasteful, nature of many diets for animals. Especially is this the case in the diets given to animals being fattened for the purposes of show. Only a small proportion of the nitrogen in these diets is stored up; the greater part passes away with the excreta, and finds its way on to the land. Precise experiments on men have shown that they can be kept in health for months on a diet far poorer in protein than that generally accepted as necessary, and the same finding, within limits, holds good for animals. On the question of food nitrogen many physiologists come into conflict with practical experience.

Theory says the quantity of nitrogen required is largely independent of the amount of muscular work performed; practice says the harder the machine is worked the more nitrogen must be given. Theory says proteins are not the source of muscular energy, the source being in the non-nitrogenous food; practice replies that may be so, but experience shows that the harder the work performed by an animal, the more richly nitrogenous must the diet be, while the amount of the food given is only to be limited by the appetite. In this matter our personal experience places us entirely on the side of practice and in opposition to theory. Why the hard-worked horse needs more nitrogen we are not prepared to explain. The suggestion that the machine works more easily and smoothly on a liberal nitrogenous diet, which stimulates metabolism, and so leads to increased oxidation, does not bring us much nearer to a solution of the problem. The fact remains that, whatever may be the energy obtainable from starch and fat, this energy is in some unknown way directed by protein. All nitrogen over and above that required for repair must not be considered a wasteful or *luxus consumption.* On the other hand, that a wasteful consumption of protein occurs where horses are not fed in accordance with the work they are performing is undoubted. Under these circumstances the excess of nitrogenous material produces clinical disturbances; we are able to recognise these in the liver disorders and diarrhœa of tropical climates, and in the lymphangitis, azoturia, and diarrhœa of temperate latitudes.

The storing-up of protein occurs in young animals and in working animals so long as the muscles are increasing in bulk. It is necessary to remember that this statement does not exclude the daily repair of the tissues. Whatever the extent of this may be—and it appears in the adult, as we have already seen, to be small, the embodiment of newly arrived protein into the body tissues is associated with an equal output of worn-out material containing the same proportion of nitrogen, so that, though the nitrogen does not vary, the tissues do.

All true proteins are capable of being used as food, but when *albuminoids*, such as gelatin, are given, though they produce the same amount of urea as an assimilable protein, the animal loses flesh. Gelatin was held of high nutritive value in diet, mainly owing to its chemical analysis and its close relationship to true protein. It took years to find out that it was worthless as a tissue builder, and the explanation of this is the absence from the molecule of tyrosine and tryptophan (see p. 368).

Function of the Nitrogenous Foods.—What we have learnt regarding nitrogenous food may now be summarised:

1. The body requires nitrogen; no diet is complete, nor can life be supported, in its absence.

2. The body having obtained its nitrogen, stores up the small amount required to replace wear and tear, and excretes the whole of the remainder, principally in the urine.

3. The body requires less nitrogen when fat or carbohydrate forms part of the diet.

4. Neither herbivora nor omnivora can live on a purely protein diet; carnivora can so live, their supply of carbohydrate being furnished by the non-nitrogenous residue.

5. The proteins are not the source of muscular energy, yet increased muscular effort must be met by an increased nitrogenous diet. In some unknown way nitrogen directs the production of energy in the muscle machine.

6. Provided the food supply be ample, variations in the amount

of work performed do not affect the excretion of nitrogen. If, on the other hand, the work be excessive and the body loses weight, the nitrogen in the urine is then increased.

7. Many animal dietaries are too highly nitrogenous, rarely for horses, commonly for cattle.

Carbon Equilibrium.—This condition implies that the total carbon leaving the body by the lungs, urine, and skin must equal the total carbon received in the food. If less is excreted, the animal gains weight; if more is excreted, it loses weight. In order to ascertain the amount of this gain or loss the subject is placed in a respiration chamber. The amount of carbon in the food, and the quantity leaving the body by the lungs and excreta, are determined. The carbon in the body is contained in the protein tissues, fat, and glycogen. As the last, under ordinary conditions, remains pretty constant, a gain or loss of carbon is attributable to a gain or loss of protein or of fat. Should it be the protein tissues the fact will be revealed by the amount of nitrogen excreted; if this fails to indicate a change, then the body fat is the source of the gain or loss.

Non-Nitrogenous Food.

Metabolism of the Carbohydrates.—Starches, dextrins, gums, and cellulose constitute the carbohydrate food of animals, and of these the most important are the starches and cellulose. The method by which these complex substances are rendered available for the body has been studied in the chapter dealing with Digestion. The carbohydrates are broken down into simpler bodies until the 'building stones' stage is reached. The building stones which the body can utilise are then selected, and by a process of synthesis they are reconstructed, the molecule passing from the simple to the complex. One of the most characteristic of these reconstructions is *glycogen*, which is stored up in the liver and muscles. It is obtained from dextrose, the comparatively simple dextrose being built up into the more complex glycogen. When required by the body the pieces are pulled apart, the glycogen reverting to the simple dextrose, the processes being enzymic in nature. It is not essential that the liver should alone be concerned in this reconstruction and pulling down of glycogen; the same process takes place independently in the muscles. Nor is it essential that the sugar from which glycogen is formed should be derived from starch, as the carnivorous animal has an abundance of glycogen, which in this case is manufactured from the carbohydrate residue of protein, or even, perhaps, from fat. It has been calculated that the total amount of glycogen which the herbivora can store up in the liver and muscles is about 4½ pounds; all dextrose assimilated over and above the glycogen storage capacity is disposed of by conversion into fat. This fat is stored up in various depots of the body for future use.

The final stages of the katabolism of dextrose are carbonic acid, water and organic acids (lactic and acetic). The intermediate stages are unknown. It is thought that the energy yielded by dextrose may be due to the oxidation of the organic acids in the tissues.

The katabolism of the other carbohydrate substances in food, cellulose and its allies, is effected by destructive fermentation. We have seen that no enzyme is known which can render this substance soluble, but it is attacked by the micro-organisms in the digestive canal. This is a prolonged operation resulting in the cell wall, but not the tough lignin, being rendered soluble. This fermentation is not of the nature of hydrolysis and cleavage, such as we have seen occurring to protein and dextrose; it results in the formation of a considerable amount of gas, carbon dioxide, methane, and a little hydrogen, together with organic acids, principally acetic and butyric. These constitute the sole contribution which cellulose makes to the body (Armsby), but the same observer pertinently asks whether these organic acids may not be absorbed from the digestive canal, and by oxidation yield energy, as happens in the case of dextrose. Such absorption may be effected by the acids combining with the alkalies of the digestive fluids, and the salts so formed being oxidised into carbonates, which appear in the urine. It is evident that if cellulose is completely destroyed in the digestive canal there can be no absorption, and consequently it is of no value to the tissues. Nevertheless, its solution permits of the escape of the cell contents, and so liberates the food-stuffs.

There are carbohydrate substances in food, belonging to the gum, pectin, and crude fibre groups, which would appear to escape complete katabolism. They appear in the urine, especially in that of ruminants, and evidently originate from coarse forage, hay, and straw, for their proportions may be increased by adding these articles of diet. The nature of these substances is unknown. The amount in the urine of sheep has been found as high as 30 per cent. of the total organic matter present, while in oxen as much as 67 per cent. of the total carbon of the urine has been found to be of non-nitrogenous origin (see p. 345).

The carbohydrates are readily oxidised, as their oxygen and hydrogen exist in the proportion to form water. One gramme (15½ grains) of carbohydrate requires 0·832 litre (50·8 cub. in.) of oxygen for the oxidation of its carbon, and produces an equivalent amount of carbon dioxide.

The function of carbohydrate food is the liberation of energy on oxidation. In the food of the herbivora it is the chief source of energy, as usually so little fat exists in vegetable bodies. Stored up in the muscles and liver, the animal carbohydrate (glycogen) is fired off by the muscles; it is replaced, as exhausted, from the dextrose of the circulating blood, and from the fat reserves of the body. During its oxidation it generates heat; 1 gramme of dextrose yields 4,100 calories, or 4·1 large calories of heat.* Oxidations are constantly going on throughout the life of the animal, for the body is never at rest. The heart muscle never ceases working, nor the muscles of respiration, nor those which carry along the contents of the digestive canal; glandular and cellular activity is always present; heat, also, is always being lost, and has to be replaced.

An undue proportion of carbohydrates in a diet 'depresses' the digestibility of the proteins, especially in ruminants. Starch or sugar added to a diet in excess, as frequently occurs in the feeding of horses with sugar or its by-products, causes less protein to be absorbed. An excess of cellulose, as in hay, straw, tubers, and roots, is believed to have the same effect. It is thought that the depression of digestibility may be more apparent than real, and explained by the carbohydrates increasing the nitrogenous excretory products in the fæces, as the result of the extra metabolism they impose on the digestive organs. Under normal conditions the excretory products in the fæces resulting from the digestion of every 100 parts of the dry matter of food, whether the diet be nitrogenous or non-nitrogenous, contain 0·4 part of nitrogen. Whether, therefore, there be less protein absorbed or more used up in metabolism does not affect the general statement that a loss of protein occurs when an excess of carbohydrate is present in a diet.

An excess of carbohydrates in a diet also depresses the digestibility of the non-nitrogenous ingredients, especially of cellulose. This is very marked in ruminants, and is explained by saying that the micro-organisms responsible for cellulose fermentation turn their attention to the more readily fermentable starch and sugar. This depression of cellulose digestion is controlled by the addition of more protein to the diet, the explanation being that in all probability the protein stimulates the multiplication of the micro-organisms, and that in consequence a sufficiency is present not only for the starch and sugar, but also for the cellulose. In connection with this question, see the remarks on non-protein nitrogen (p. 368).

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* A *large* calorie is the amount of heat necessary to raise 1 kilogramme (2·2 pounds) of water 1° C. (1·8° F.), and is sometimes named a kilocalorie.

Metabolism of the Fats.—We have seen that in most articles of vegetable food the amount of fat is small, though in some seeds—cotton, linseed, and such like—it exists in large amounts. Some of the material existing in vegetable food described in analyses as 'ether extract' is not necessarily all fat; waxy and resinous matters are frequently included which are not of the nature of fat. Both in animal and vegetable bodies *Lecithins* are found; these are substances related to fat, but differ from it in containing nitrogen and phosphorus, though they yield fatty acids on hydrolysis as true fats do.

The digestion of fat has already been studied; broken up in the intestines into fatty acids and glycerol, it is resynthesised in the intestinal wall under the influence of the ferment lipase, and in a state of emulsion enters the lacteals. On reaching the blood, however, the condition of emulsion ends, and the fat then being soluble, easily reversible, filtrable, and dialysable, in this condition is transported to the tissues. Here it returns to its condition of emulsion by a process not understood, and a body fat, peculiar to each animal, is stored up in the fat depots. The fat of horses is soft, that of sheep hard, the fat of cattle occupying a midway position. A dog fed on hard fat converts it into canine fat, which is soft; cattle fed on fluid fats convert them into semi-hard body fats. Experiments, however, show that foreign fats used for feeding may be detected in the tissues. Oil cake and linseed oil may produce an oily milk, and dogs constantly fed on mutton fat may accumulate this type of fat in their tissues; pigs receiving too large a proportion of fluid fat in the diet accumulate a soft fat, which boils away on cooking. It is generally believed that green food, hay, and carbohydrates produce a hard body fat, while grain foods, such as oats, conduce to a soft fat. It is curious that two animals so closely alike in their digestive arrangements and diet as the ox and sheep should each produce a different fat; the hard, white fat of the sheep is very different from the yellow and softer fat of cattle. The yellow colour is due to *carotin*, a pigment found in leaves.

The food-fat is not the only or principal source of fat in the body; great stores of fat exist in the bodies of animals receiving a trifling amount of fat in their food. The fat is derived from the carbohydrates, and this explains why a cow produces more fat in her milk than she receives in her food. It was Gilbert and Lawes who first demonstrated the production of fat from carbohydrate; it is a remarkable physiological synthesis, the seat of which is unknown.

Fats contain energy in a concentrated form, yielding more per unit than any other food substance; they are oxidised with difficulty, as they possess in their constitution only one-eighth

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of the total oxygen required for the oxidation of their hydrogen to water. One gramme of fat requires 2·8875 litres (176 cub. in.) of oxygen, and produces 1·434 litres (87·5 cub. in.) of carbon dioxide. By its oxidation heat is produced, 1 gramme of fat yielding 9·3 large calories.

The way in which the fat is taken up from its body reserves for utilisation is unknown. Presumably there is a reversal of the process by which it was deposited in the tissues, and when the stage of fatty acids and glycerol is reached the fatty acids are oxidised step by step, with the production of carbon dioxide and water. In the decomposition of the fatty acid, oxidation takes place at the second carbon atom from the carboxyl group —*i.e.*, the β-position.

The **Function of the Non-Nitrogenous Foods** may be summarised as follows:

1. The fats supply a considerable amount of energy in a small bulk, and in the forms of cholesterin, lecithin, phosphatides, etc., they are essential constituents of the body protoplasm.

2. The carbohydrates are also carriers of energy, and as more carbohydrate than fat can be consumed they furnish the greater part of the energy of the body.

3. Too large a proportion of starch or sugar in a diet depresses the digestibility of protein and cellulose.

4. The fats and carbohydrates of the food are worthless, as energy producers, without the presence of protein; it is this which enables the muscle-machine to convert the chemical energy of the non-nitrogenous substances into mechanical work.

Growth.—The rate of growth of the fœtus is considerable; from birth to adult age the rate diminishes at first rapidly, then slowly. The metabolism of growth is only imperfectly known. The gain in weight of the very young animal is principally water, and in a much less degree protein; as maturity approaches the percentages of water, protein, and ash stored up decrease, while that of fat increases.

We have already seen (p. 368) that there are certain amino-acids necessary for growth, and that in their absence normal growth is not attained. *Lysine*, for example, appears indispensable, its absence in maize rendering the grain unsuitable for young animals; *tryptophan*, too, in which maize is also deficient, is of considerable importance in growth. The deficiency of maize in these two amino-acids is further associated with a deficiency in salts and in *vitamines*, especially in the vitamine soluble in fat, which is known to be essential to growth.

The protein requirements of the young animal are of two kinds: for maintenance and for growth. The rapidly growing tissues make a considerable demand on protein, and the protein so utilised does not find its way out of the body in the form of waste nitrogenous products. As growth diminishes and maturity approaches the demand for protein becomes less, and in consequence a larger amount of its degraded products appears in the urine. Nevertheless, experiment shows that only a certain proportion of protein can be utilised for maintenance and growth, and that all over and above that amount is metabolised and finds its way out by the urine. Experimental inquiry also indicates that liberal feeding does not materially promote growth, though it may lead to the deposition of fat, and suggests the conclusion that the amount of protein hitherto given has been unduly high. But, precisely as in the case of the protein supply for adult animals referred to at p. 370, practice is here opposed to science. It is the general experience of graziers and breeders of stock that an insufficient food supply stunts growth, and that a liberal ration increases it (see Fig. 111). In the light of modern discovery, it may be urged that a ration deficient in quantity is also deficient in vitamines, and that the liberal ration occasions growth because, quite apart from the protein content of the diet, the vitamine factors for growth exist in it in larger quantities. It would be unwise to dogmatise as to the precise agents at work, but this can, at least, be definitely

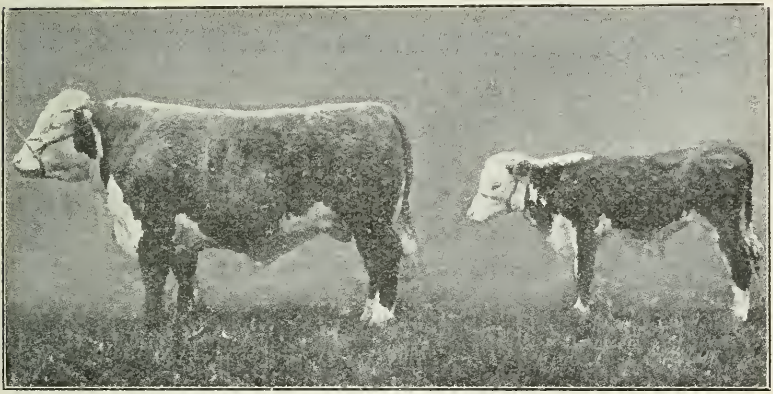

FIG. 111.—EFFECT OF FOOD SUPPLY ON DEVELOPMENT (F. B. MUMFORD).*

These animals were born on the same day. The one on the left was fed generously from birth, and weighed 1,610 pounds when two years old. The animal on the right was limited in the amount of food supplied, and at two years old weighed 361 pounds.

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* 'The Breeding of Animals,' New York, 1919.

stated, as the result of the impressions of a lifetime, that a stunted race of animals could be produced at will by underfeeding the young stock. During the period of intra-uterine life the result of underfeeding the mother is to affect seriously the full development of the progeny. Underfeeding the young animal does not completely arrest growth, for the skeleton slowly increases in size at the expense of the other tissues. The influence of underfeeding on growth has been submitted to experimental inquiry in the U.S.A.* It was found that it reduced the capacity to grow, but that after a period of partial starvation, lasting a year, an abundant food supply permitted active growth to take place, though as the result of the previous hard life the size of the adult animal was permanently diminished.

A proportion of fat in the diet of growing animals is regarded as indispensable, but it is not unlikely that the vitamine soluble in fat is principally concerned in the growth of the animal, though it does not exist in vegetable oils. It is, however, abundantly present in the leaves of grass, clover, and almost certainly in hay.

Fattening of Animals.—There are certain fat-reserve depots natural to the animal, on which, under ordinary circumstances, little or no drain occurs; such are found beneath the skin, in the peritoneum, around the kidneys, in the mesh of the omenta, and surrounding the base of the heart. The chief means to induce the laying on of fat is a liberal diet and freedom from exercise and work. The farmer feeding for beef or mutton understands the value of keeping the animals as quiet as possible, and recognises also that there are certain breeds which have a distinct predisposition to store up fat. Further, he learns how necessary it is to introduce animals gradually to a fattening diet until toleration is established, and he knows from practical experience that he will not succeed in fattening within a reasonable time unless to the diet of carbohydrate and fat he also adds proteins liberally. The measure of the diet is the animals' appetite; they can never eat enough to please the feeder, who cheerfully accepts the heavy initial outlay, as he knows the subsequent saving in time effected. It is at this point that science and practice again come into conflict. It is urged that most of the diets given to fattening animals are wastefully nitrogenous. This is certainly true where 'show' condition is aimed at; the obesity then produced in cattle, sheep, and pigs is a pathological condition repugnant to common sense, and the outcome of a barbarous fashion. All modern experimental inquiry directed to ascertain the most suitable protein content of a fattening diet shows that animals may be fattened on a diet containing far less protein than that advocated some years ago.

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* T. F. Trowbridge in F. B. Mumford's 'Breeding of Animals.' New York, 1919.

In the investigations of Lawes and Gilbert, tables of which are given below, the animals were permitted to make their own choice of food substances, and the amount of protein and non-nitrogenous material was quite unrestricted.

The consensus of opinion is in favour of castration as facilitating fattening. It is quite certain, however, that geldings have no greater disposition to accumulate fat than mares; if castration favoured fattening among horses, there would be no need for that constant striving after fatness instead of 'fitness' which is so characteristic of all who have charge of them. There are, of course, some animals which have a tendency to store up fat and others which never do any credit to their 'keep,' but this is an individual peculiarity not explained by castration. It has been suggested that the accumulation of fat observed in castrated animals is due, not to an increased production of fat, but to a failure to utilise it. It is thought that the liver prepares the fat for utilisation under the influence of a hormone secreted by the testicle; if this is the case, the liver in castrated animals should be reduced in size, and this has been found to be the case in the cock. Observations on other animals are wanting.

Reference has been made at p. 258 to the fact that in animals other than herbivora the liver acts as an important fat depot. This is the case in man and carnivora; it is well known to occur in the goose; the rabbit also, during late pregnancy and early lactation, may show the same condition. In these cases the liver obtains its store of fat from the adipose tissues, the transport probably taking place in the form of fatty acids and glycerol; the higher fatty acids are desaturated in the liver and then broken down into lower fatty acids; these in turn are transported to the active tissues for combustion.

Storage of Tissue.—Every diet for fattening must contain the food principles we have been considering—viz.:

Protein.
Carbohydrate.
Fat.
Vitamines.
Salts.

It is interesting to learn in what proportion these are stored up in animals being fattened, also the amount of food required for a definite increase in weight, and the rate at which that increase occurs. The following tables are compiled from the classical experiments of Lawes and Gilbert, which extended over a period of twenty years:

TABLE I.

Metabolism occurring while the Body is increasing its Weight by 100 Pounds.

	Oxen.	Sheep.	Pigs.	Remarks.
	lbs.	lbs.	lbs.	
Water-free food required	1,109	912	420	Oxen consume more food and produce considerably more excreta than sheep, and sheep very much more than pigs, during the period occupied in adding 100 pounds to the body weight. This period for oxen is five or six, and for sheep three or four times as long as for pigs (see Table IV.). The nature of the stored-up matter is shown in Table II. The maintenance and internal work was highest in pigs, rather less in oxen, and still less in sheep.
Utilised in internal work	636	548·5	276·2	
Excreta produced	404·4	291	70	
Stored up, water-free	68·6	72·5	73·8	

TABLE II.

Proportion of Food Principles stored up for Every 100 Pounds increase of Body Weight.

	Protein.	Fat.	Salts.	Total Water-free Substance stored up.	Remarks.
	lbs.	lbs.	lbs.	lbs.	
Oxen -	9·0	58	1·6	68·6	Oxen store up the most protein, pigs the most fat, and sheep the most salts. Oxen store up $\frac{1}{16}$ of their food, sheep rather more than $\frac{1}{12}$, and pigs nearly $\frac{1}{6}$. The chief increase in body weight is fat. Sheep and oxen develop bony structure during the fattening process more than pigs.
Sheep -	7·5	63	2·0	72·5	
Pigs -	7·0	66	0·8	73·8	

TABLE III.

Metabolism of 100 Pounds of Water-Free Food.

	Oxen.	Sheep.	Pigs.	Remarks.
	lbs.	lbs.	lbs.	
Utilised in internal work	57·3	60·1	65·7	Oxen produce more excreta than sheep, and sheep very much more than pigs, while metabolising 100 pounds of water-free food. During this process the internal work is highest in pigs and lowest in oxen, for the reason that pigs assimilate between three and four times more from a given quantity of food than oxen and sheep.
Excreta produced	36·5	31·9	16·7	
Stored up:				
Protein -	0·8	0·8	1·7	
Fat and carbohydrate	5·2	7·0	15·7	
Salts - -	0·2	0·2	0·2	
	100·0	100·0	100·0	

TABLE IV.

Metabolism, calculated on 100 Pounds of Body Weight, which occurs Week by Week during the Process of storing up 100 Pounds of Food Substances.

	Oxen.	Sheep.	Pigs.	Remarks.
	lbs.	lbs.	lbs.	
Water-free food consumed per 100 pounds body weight	12·5	16·0	27·0	In every 100 pounds of body weight oxen and sheep consume less food than pigs, and in consequence use up less on internal work. The excreta produced per 100 pounds of body weight is almost identical in the three animals. The percentage of increase in body weight is markedly different; consequently, it takes oxen five or six, and sheep three or four times as long as pigs to add 100 pounds to the body weight.
Utilised in internal work	7·16	9·62	17·74	
Excreta produced	4·56	5·10	4·51	
Increase in body weight	1·13	1·76	6·43	

TABLE V.

Amount assimilated for every 100 Parts of Each Substance of Food consumed.

	Oxen.	Sheep.	Pigs.	Remarks.
	lbs.	lbs.	lbs.	
For every 100 pounds of protein	4·1	4·2	13·5	This is a digestion experiment. The food of the pig is much more concentrated than that of the ox and sheep, but the two herbivora, fed on identical foods, show a marked difference in the powers of assimilation.
For every 100 pounds of fat and carbohydrate	7·2	9·4	18·5	
For every 100 pounds of salts	1·9	3·1	7·3	
	13·2	16·7	39·3	

TABLE VI.

Amount of Food required to produce One Pound increase in Body Weight.

	Oxen.	Sheep.	Pigs.	Remarks.
	lbs.	lbs.	lbs.	
Linseed cake -	2	2·5	—	The 43 pounds for oxen weighed 11 pounds in a water-free condition. The 45 pounds for sheep weighed 9 pounds in a water-free condition. The 5 pounds for pigs weighed 4·2 pounds in a water-free condition.
Clover hay -	6	3·0	—	
Swedes - -	35	40·0	—	
Barley meal -	—	—	5	
	43	45·5	5	

Metabolism of the Salts.—The salts of the body direct its metabolism; they are connected with assimilation, secretion, excretion, and the building up of the skeleton; moreover, they maintain the body fluids at their normal reactions—*i.e.*, the blood and lymph at neutrality, the saliva alkaline, the gastric juice acid, the intestinal fluid alkaline, and the urine alkaline or acid, depending on the species of animal. The salts also regulate the water-flow from blood to tissues, and *vice versa ;* they play an essential part in blood-clotting, rhythmical contraction of the heart, irritability of muscle and nerve, milk curdling, and growth. Salts are always being excreted, and must be replaced. This is done through the medium of the food, which, if salt-free, though suitable in every other respect, would fail to support life; in fact, animals fed with salt-free food die earlier than those receiving no food. An abundance of salts is found in vegetable food. The plant is unable to grow without *potassium* or *calcium* ; *phosphorus* and *sulphur* are needed by it for the transport of its protein, *iron* for the chlorophyll, *magnesium* for the seed.

The distribution of the salts throughout the body structure is remarkably regular, sodium being found in the blood-plasma, potassium and iron in the red cells, sulphur in hair and horn, potassium in muscle and sweat, sulphur in protein, calcium and phosphorus in bones, protein and some fats. When a deficiency in salts occurs, the body for some time apparently draws on its own store, and then nutritive changes follow. These are more likely to show themselves earlier in young than in adult animals, but the influence of inorganic food on the nutrition of the skeleton is little understood.

The chief salts used by the herbivora are those of *potassium*, while salts of *sodium* are used by the carnivora. The ratio of potassium to sodium salts in the diet is a question of importance; potassium salts, when in excess, cause a withdrawal of sodium salts from the body, and nutritional diseases of the skeleton in horses have been associated with an excess of potassium salts in hay. This excess has involved a loss of sodium, while the loss in sodium has in turn produced losses in calcium and phosphoric acid. The alkalinity of the urine of herbivora is due to the presence in the food of an excess of alkaline ash ingredients over acid ash ingredients. By errors in diet, as, for instance, feeding a horse on oats only and no hay, the urine may be rendered acid. The protein of the oats, containing sulphur and phosphorus, produces acids in the body which have to be neutralised. The salts in the hay furnish the necessary alkali, and in its absence or insufficiency the urine becomes acid. Maize is a food very poor in calcium, and would be quite unfitted for young growing animals but for the requisite calcium salts being furnished by hay or grass. It has been found experimentally in the feeding of pigs on maize alone that these animals failed to grow, while the addition of salts to the maize enabled nearly normal growth to be made. For instance, 5 grammes of calcium carbonate added to 1 kilogramme of maize has changed a loss of calcium and of phosphorus into a gain (Armsby).

It is generally considered that the herbivora require the addition of sodium chloride to the food; this has been scientifically explained by saying that, as potassium salts normally withdraw sodium from the body, the latter is replaced by the addition of common salt. The wild herbivora are reported to travel considerable distances to obtain the necessary sodium from 'salt-licks.' This may be true, but the fact remains that horses may remain fit and well for years without common salt being added to their diet, the little already in the food being ample; the same statement has recently been made in connection with dairy stock.

Potassium and sodium salts are excreted by the urine, and in the horse by the skin. The amount of potassium in sweat is so considerable that the hair feels sandy when the coat has dried. In the ruminant the loss of potassium by sweat is trifling, but the considerable amount of hippuric acid furnished by this species makes a heavy draft on the alkali of the body, as this acid is mainly excreted in the form of hippurate of potassium.

Calcium and *Magnesium*, especially the former, are required for the nutrition of the skeleton. Calcium abounds in the body, magnesium exists only in small proportions. The precise manner in which calcium performs its functions is unknown. It is excreted in the milk—cows may even excrete more than they receive—and by the urine and fæces; in the dog it has been shown to be absorbed in the anterior part of the digestive canal, and excreted in the posterior portion. Clover hay contains more than five times as much calcium as timothy hay, hay contains more than oats, but straw contains more than hay. Food poor in calcium leads to deficiencies in growth and changes in the skeleton. Rapidly growing animals, such as pigs, fed on grain rations are especially liable to such changes, but in the herbivora on ordinary food no such changes are likely to occur. There is far more calcium in the food than horses require; the surplus is unabsorbed, and is excreted with the fæces. Occasionally it fails to be excreted, and forms calculi, a foreign body, nail or pebble, being an invariable nucleus. Other intestinal calculi are due to ammonio-magnesium phosphate and lime being entangled in the fine insoluble hairs on the kernel of oats, and forming a felt-like mass of remarkable lightness.

The calcium carbonate excreted in the urine of the horse is always in excess of what can be kept in solution. The precipitation occurs in the kidneys, and the solid material is excreted in suspension; in cattle the calcium in the urine remains in solution.

Sulphur enters the body principally as *cystin* in the protein. Cystin yields taurin, which is necessary for the bile. Both of these substances are readily oxidised in the system, and yield sulphuric acid, which, either in combination with phenol, derived from putrefactive processes in the intestine, or as salts, finds its way out of the body by means of the urine. An excess of protein may lead to an acid reaction of the urine, as mentioned above and in the chapter on the urine. A pound of protein, having the composition of serum albumin, if fully oxidised in the body, would yield nearly 1 ounce by weight of concentrated sulphuric acid (Armsby). There can be no doubt that much sulphur escapes unacted upon from the body by means of the fæces, and does not contribute to the production of acid in the body. The origin of the *neutral sulphur* of the body is unknown.

Phosphorus is introduced into the body in organic combination with phospho-protein, nucleo-protein (lecithin), as phosphatides in the phosphorised fats, and in inorganic combination as phosphates. An important source is the organic phosphorus; it is believed that most of this enters the blood as phosphoric acid, the acid radicle being split off under the influence of the enzymes of the digestive juices. Experimental inquiry shows, however, that the tissues are capable of using inorganic phosphates in the production of the complex phosphorus-containing compounds found in the body. The skeleton is the chief seat of the deposition of phosphorus. Far more phosphates are taken in with cereals (oats, bran) than are required for body purposes; they are accordingly excreted with the fæces, and in the horse, as just mentioned, are a cause of intestinal calculi. Feeding-stuffs containing an excess of phosphorus either lead to the production of acid in the blood, which necessitates neutralisation, or else they produce an acid ash in the urine. The neutralisation in the blood is effected by sodium bicarbonate. In carnivora the urinary ash is acid, the acidity of the fluid being due to the acid phosphate of soda. In herbivora the proportion of phosphates in the urine is small; in all probability, after having done their work, they are excreted as phosphates into the intestinal canal, such as has been observed in the case of calcium in the dog, though in dairy stock there is a large outlet through the secretion of milk.

Iron and *Iodine* enter the body with the food, mainly in organic combination; they are required, the one for the blood, the other for the thyroid gland, but their metabolism is unknown. Inorganic iron and iodides are capable of replacing them.

The **storage of salts** by the growing animal is a question of considerable importance; the experiments of Lawes and Gilbert have revealed the amount of ash ingredients retained by animals during growth, as will be seen from the following table computed by Armsby:

AVERAGE RETENTION BY GROWING ANIMALS OF ASH INGREDIENTS PER DAY.

	Yearling Cattle.	Yearling Sheep.	Six Months' Old Pig.
	Grammes.	Grammes.	Grammes.
Potassium - -	1·64	0·20	0·45
Sodium - - -	1·08	0·12	0·22
Calcium - -	15·37	1·29	2·11
Magnesium - -	0·50	0·05	0·09
Phosphorus - -	8·14	0·71	1·27
Chlorine - -	0·59	0·10	0·16

The percentage of salts retained in the body decreases from birth to maturity; with young animals 53 per cent. of the total ash of milk may be assimilated, while of individual salts absorbed those of calcium may stand as high as 97 per cent., and of phosphorus 72 per cent. Both the organic and inorganic phosphorus of food is assimilated; even in the coarser foods, such as hay and straw, 50 per cent. of the phosphorus may be taken up.

The whole question of the metabolism of salts in young and adult animals, under all conditions of growth, food production, and work, requires investigation. What is very clearly known is the constant production of acid in the body, and the necessity for its neutralisation if the blood and lymph are to remain normal. We have seen how the acid produced by the katabolism of protein is neutralised by means of the ammonia produced from the amino-acids, ammonium salts being excreted by the urine.

We have also seen how the loss of salts from the body is influenced by the composition of the ash of the food, an excess of acid or basic elements in these affecting the gain or loss of sulphur, phosphorus, and calcium. The alkali ratio of the salts of the food is another example of this, an excess of potassium salts leading to a loss of those of sodium, calcium, and phosphoric acid.

Summary of Ash Metabolism.

A general account of the metabolism of the salts in the body is somewhat as follows: The source of the salts is the food. In green or fresh vegetable bodies these are held in simple solution in the form of chlorides, sulphates, carbonates, phosphates, etc. Certain elements, such as iron, iodine, phosphorus, and sulphur, may also be held in organic combination. If the food be dry the salts may exist in crystalline form; the grinding in the mouth exposes them to the solvent action of the saliva, and this process of solution is continued in the stomach or in the rumen of ruminants. What escapes the saliva is dealt with by the gastric juice; especially is this true of the calcium salts, since the saliva is already saturated with these (p. 168).

In the digestive canal as much saline matter is taken up as the system requires. It is by no means the full amount contained in the food, for much is excreted with the fæces unacted upon. This is especially the case in the horse in respect of calcium and phosphorus. The salts are taken up into the system by the process of diffusion, and are carried in the blood both by the plasma and cellular elements. Each tissue selects with unerring accuracy the salts which it requires either for building up or for secretory purposes. It is reasonable to suppose that some of the older salts in the tissues are displaced; perhaps some are got rid of by being utilised for glandular secretions, those not so required passing into the blood and being excreted through the kidneys. There is a great deal of evidence to show that a storage of salts occurs in both the hard and soft tissues of the body, and that it is this store which provides the salts in those cases where there may be a temporary shortage in the food.

The various secretions constitute an important source of loss; the salts contained, for instance, in milk and sweat, leave the body for good, while others—those, for example, in the digestive fluids—are reabsorbed and eventually got rid of by the kidneys, or if not reabsorbed gain exit by the fæces.

The elements which are held in organic combination, as, for example, iron in hæmoglobin, iodine in the thyroid gland, phosphorus in nuclein and lecithin, and magnesium in chlorophyll, are got rid of by the various secretions. Thus the worn out red cells get rid of their iron in the spleen (?), the thyroid secretion uses up iodine, and the iron and magnesium contained in chlorophyll are got rid of through the intestinal canal and, in the horse, partly by the skin. It is now ascertained that the inorganic salts of the food may furnish the elements required by the organic combinations; that phosphates serve as a source of organically bound phosphorus; that iron salts can supply what is required by hæmoglobin, and iodides supply the iodine for the thyroid.

It is easy to understand that the salts required day by day are readily available from the food, as there is, as we have seen, already an excess present. Those required for an unexpected secretion—such, for example, as a profuse sweat after a gallop—are no doubt taken up from the store in the tissues, the muscles, for instance, furnishing the large amount of potassium contained in sweat, in the same way that solid tissues may furnish the salts required for milk.

The saline matters for excretion, having reached the kidney, pass through the glomerular filter in solution. It does not follow that the various salts in the uriniferous tubes are all excreted with the urine. According to Cushny's theory, some would be reabsorbed by the cells of the tubules in order that the blood may retain its normal saline concentration, and be finally excreted when they can be spared, but the larger part would pass out of the body with the urine. It will be remembered that the fluid as filtered by the glomerulus is extremely dilute, and that in the tubules water is reabsorbed. In the case of the horse this concentration throws out of solution a great deal of calcium carbonate, which accordingly, as we have seen, is deposited in the pelvis of the kidney and produces a turbid urine. Under pathological conditions other salts may be precipitated in the tubules or pelvis of the kidney—for example, those of uric acid.

Organic acids enter the body by means of the food—silage, for example, which contains *acetic, butyric,* and *lactic acids.* Such are neutralised by the digestive fluids, and after their absorption and oxidation to carbon dioxide and water the bases are returned to the body. Some organic acids—*tartaric, malic,* and *oxalic*—are not readily oxidised, and carry off the bases or even calcium from the body. Adult ruminants are capable of dealing with the acids of their food by fermentation in the rumen, and consequently the loss of bases observed in horses, young ruminants, and swine is not so evident in adult ruminants. Organic acids are also produced in the body as the result of the fermentation of cellulose. It is believed that these may be oxidised, and so utilised by the system, but before this can occur they withdraw bases from the body, and so tend towards the production of acidosis.

Accessory Food Substances.*

Vitamines.—These bodies—there are probably several—have been identified only within the last few years. They are chemical substances contained in fresh food in extremely minute proportions, and their function would appear to be, in some way or other, to direct metabolism. They are absolutely essential in a diet, and to their absence are due the diseases in man known as beri-beri, pellagra, scurvy, and rickets. If a man be fed on a diet of pure protein, purified starch, pure sugar, and a vegetable fat, he will die, though the diet is wholesome and digested. If to the diet be added a small quantity of a watery extract made from wheat grain, or from the germ of wheat, or from the 'polishings' (husk) of rice, and if an animal fat be substituted for a vegetable fat, growth and vitality are maintained.

The diseases due to the absence of vitamines from the diet are classed as *deficiency diseases.*

At the present time there are only three vitamines which have been isolated. One is soluble in water, and is provisionally known as water soluble 'B'; a second is contained in animal fats (lard excepted), such as milk fat and cod-liver oil, and in the green portions of plants; it is known as fat soluble 'A.' The third vitamine is found in fresh vegetables and in the juice of fruits, especially oranges and lemons; it possesses antiscorbutic properties. All the vitamines must be present in a diet, and all are primarily derived from the vegetable kingdom directly or indirectly. In plants they are produced by synthesis.

Water soluble 'B,' or *antineuritic factor,* was the first vitamine discovered. It is found in all natural food-stuffs, but its principal sources are the seeds of plants and the yolk of eggs; this suggests its importance in connection with the growth of the embryo. The cereals contain this vitamine in the peripheral layer of the seed and in the seed envelope, but especially in the germ. When grain is decorticated by milling, the vitamine is lost, which explains why beri-beri is due to feeding on milled rice and can be cured by the administration of water soluble 'B' or by the use of unhusked rice. The pulses contain it throughout the seed, but only in moderate amounts. Yeast contains it in abundance; flesh contains very little.

There is no important reserve store of this vitamine in the body, so that its absence from a diet is felt very early, especially by young growing animals, which cease to grow and lose body weight. The body weight of adults also suffers, and muscular inco-ordination appears. Fig. 112 is a photograph of a young rat suffering from a deficiency of water soluble 'B'; the hind legs are paralysed and stretched out behind. Nevertheless, this animal recovered under the employment of yeast extract, and in twenty-four hours was able to walk about. Pigeons paralysed in the legs and wings as the result of deprivation of this vitamine recover in a few hours after its administration by the mouth.

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* In the compilation of this section the valuable Report of the Committee on "The Present State of Knowledge concerning Accessory Food Factors (Vitamines)," 1919, has been largely drawn upon. I am indebted to its chairman, Professor F. Gowland Hopkins, D.Sc., F.R.S., and to the Controller, His Majesty's Stationery Office, for permission to reproduce Figs. 112 and 113.

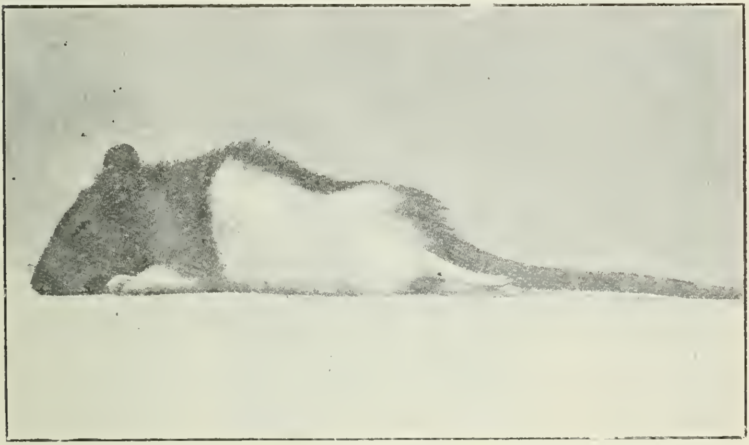

FIG. 112.—A YOUNG RAT SUFFERING FROM A DEFICIENCY OF WATER SOLUBLE 'B.'

The hind limbs are paralysed and stretched out behind. This animal walked about with ease twenty-four hours after a dose of yeast extract had been given by the mouth. (Committee Report on Vitamines.)

H. H. Green* is of opinion that water soluble 'B' vitamine is chiefly concerned in the metabolism of the food. The larger the quantity of food consumed, the more vitamine is required to metabolise it; if the diet is vitamine-poor, the greater the consumption the earlier do deficiency symptoms appear. He states that the vitamine requirements should be estimated, not so much from the point of view of a daily physiological minimum, as from that of a minimum quantity per unit of food metabolised, a fixed quantity of digested food requiring a fixed minimum of water soluble 'B' for its combustion.

Green regards the requirements of men and pigeons as very similar, and much higher than those of cattle. He fed cattle almost exclusively on 'polished' rice for over a year without producing deficiency disease.

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* Department of Agriculture, South Africa, Fifth and Sixth Reports of the Director of Veterinary Research, 1919.

Fat soluble 'A,' or *antirachitic factor*. This vitamine is necessary not only for growth in young animals, but for the maintenance of health in adults. It is contained in fats of animal origin, including fish oils, but not lard; it is practically absent from vegetable oils. Green leaf vegetables contain it, but it is deficient in root vegetables. Except in the case of the pig this vitamine is stored in the body, so that there is a reserve in the fat depots on which the animal can draw for some time.

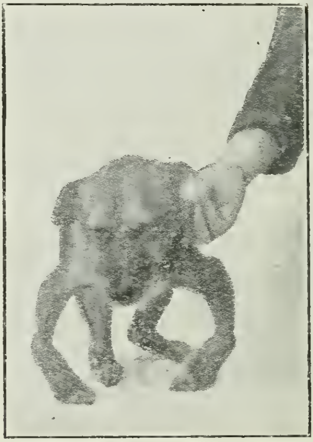

FIG. 113.—EXPERIMENTALLY PRODUCED RICKETS IN A DOG.

This animal received a diet of 175 c.c. whole milk, bread *ad lib.*, and 10 c.c. linseed oil per diem. Time of experiment, five and a half months. Increase in weight during that period, 2,670 grammes. (Committee Report on Vitamines.)

E. Mellanby's researches on rickets in dogs show that the disease may be prevented by suitable additions to the diet, especially by giving cod-liver oil, which contains fat soluble 'A' in large quantities. Mellanby has shown that a puppy taken from its mother at six weeks old will develop rickets within six weeks if placed on a diet of separated milk, white bread, yeast, orange juice, and linseed oil. Fig. 113 shows rickets in the dog experimentally produced. In this case whole milk was substituted for separated, which explains the delay in the onset of the disease.

Noel Paton and his fellow-workers hold that evidence of rickets being due to dietary deficiency alone is still lacking, and the possibility that it may be primarily an infective disease must be borne in mind.

The *antiscorbutic factor* is contained in fresh vegetables, and

ERRATUM

The statement that the fat-soluble vitamine is not stored in the living body of the pig is incorrect. It is not found in lard, being destroyed by the temperature at which this product is obtained.

To face p. 390.

to an extent in animal tissues. It is richest in cabbage, swedes, turnips, lettuce, oranges, and lemons; potatoes, carrots, mangolds, and lime-juice only contain inferior amounts, while in milk and meat it is of low value. It is deficient or absent in all dried vegetables, cereals, and pulses. Scurvy may be produced experimentally in guinea-pigs by withholding the vitamine; the symptoms appear about the twentieth day, and death occurs ten or twenty days later. The account of the post-mortem appearances of animals so affected reminds one of those presented by cattle, sheep, goats, and occasionally by horses in South Africa in a disease described by D. Hutcheon* as *osteomalacia*. He regarded this affection as being due to the absence of calcium phosphate from the food. In these cases there was also a train of nervous symptoms associated with paralysis of the hind extremities.

It is stated† that guinea-pigs fed on whole oats, hay, and water, even with the addition of cod-liver oil, develop scurvy, but that on the hay being replaced by straw the disease is cured. We do not know with precision the vitamines in ordinary feeding-stuffs used for animals. A diet of oats and bran does not permit of the growth of guinea-pigs.‡ In fact, the seeds of any plant —wheat, oats, maize, beans, peas, etc.—do not furnish the growth or fat soluble 'A' factor, but if the whole plant be given there is a compensation, for it has been shown§ that the leaf may make good the deficiency in the seed. This occurs in the case of clover, the leaves of which contain an abundance of fat soluble 'A.' Clover also contains water soluble 'B.' Timothy in the green state contains both factors. It is almost certain that fat and water soluble factors are not destroyed in hay, but exact information is not yet available.

Nothing definite is known of the position of *osteoporosis* of the horse in its relationship to deficiency disease.

The chemical nature of the vitamines is unknown; they are distinguished by their solubility in water and other agents, and by the effect of heat on them; for instance, the antiscorbutic vitamine is destroyed by heat and by drying, which explains why it is absent from preserved vegetables.

Water.—The amount of water found in the same class of tissues is very constant. The muscles of creatures as far removed from each other as the pig and the snail, the ox and the lobster, contain 78 to 79 per cent., and other tissues are equally uniform.

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* Report of the Colonial Veterinary Surgeon, Cape of Good Hope, 1903.

† H. F. Hess and L. J. Unger.

‡ H. Chick, E. M. Hume, and R. F. Skelton.

§ E. V. McCollum.

Under the conditions of rest and work varying quantities of water are lost, and in hot weather the loss is still further increased. It has been calculated that a man may lose water at the rate of 5 per cent. of his body weight on a hot day, and that muscular work in hot weather may increase the output of water as much as six times; but we are not aware of any exact experiment on this question on animals, though we know that in the case of horses the loss of water is considerable. Of the total water received in the food or consumed, the bulk passes away by the kidneys; during work a considerable amount is lost by the skin and lungs, and less in consequence passes by the kidneys.

The very constant proportion of water in the tissues shows that the consumption of excessive amounts of fluid does not lead to storage. Adjustments are readily effected, and the excess of fluid in the blood is rapidly got rid of. All animals withstand a deficiency of water badly; the horse is probably the weakest in this respect, and shortage of water is far more immediately serious for any horse than shortage of rations. A thirsting animal dies when it has lost 10 per cent. of its body weight in water, though 50 per cent. of its protein and the whole of its fat will disappear before death from starvation ensues. A man may avoid putting on weight by keeping himself short of fluid, and horses will rapidly lose condition by having their water supply limited. Without sufficient water neither rumination nor intestinal digestion in any of the herbivora can go on; the contents of the rumen of the ox and of the colon and cæcum of the horse must be kept fluid, and much of the water consumed is devoted to the purposes of digestion. Further, the blood must be kept fluid and concentration avoided; a concentrated blood draws on the tissues for fluid, but later on this source dries up, and unless dilution of the blood be effected, death is only a matter of time, and in horses undergoing severe exertion only a very short time elapses before complete collapse occurs.

Starvation.—When an animal is starved it lives on its own tissues; in the herbivora the urine becomes acid, hippuric is replaced by uric acid, and the secretion becomes transparent. We have seen that the elimination of nitrogen by the starving animal at first falls rapidly, then gradually. During starvation the carbon dioxide excreted falls in amount, and the oxygen absorbed becomes reduced, though not in proportion to the fall of carbon dioxide. If water be given, life is considerably prolonged; a horse receiving water may live thirty days without food. It is notorious that herbivora, though they lose less protein during starvation than carnivora, do not withstand starvation so well; nor need we go so far as a starvation experiment to ascertain this fact. When men and horses are being hard worked, the loss in condition amongst the horses sets in early, and is extremely marked for some time before the men show any appreciable muscular waste.

Horses have been known to live without food or water for as long as three and dogs for four weeks; but it is said that if horses have suffered fifteen days' starvation, the administration of food after this time will not save them.* Colin records an experiment where a horse weighing 892 pounds died after thirty days' starvation, being allowed only 2½ pints of water per diem. The animal was nourished on its own tissues, the daily loss in weight being 5·9 pounds, which must be considered as exceptionally small. Dewar† records two remarkable instances of the length of time sheep will withstand starvation; in one instance eighteen sheep were buried in the snow for six weeks, and only one died. In the second case seven sheep were buried for eight weeks and five days, and all were recovered alive, and eventually did well.

In some very accurate experiments on a starving cat, it was shown that the principal loss occurred in the fat, 97 per cent. of which disappeared in thirteen days. The following table shows the percentage of dry solid matter lost by the tissues:

Fat	97·0 per cent.
Spleen	63·1 ,,
Liver	56·6 ,,
Muscles	30·2 ,,
Blood	17·6 ,,

The loss in the glandular organs was very heavy; next followed that in the muscles, and then that in the blood. The heart-muscle and central nervous system suffered no loss; evidently their nutrition was kept up at the expense of other tissues of less importance. Old animals bear starvation much better than young growing ones, as their requirements are smaller.

Maintenance and Production Rations.—It is evident that the food required for the internal work of the body must be considered apart from that needed for production, and a large number of experiments have been made to ascertain the amount required for the former purpose. This internal work we have seen consists in respiration, the action of the heart, mastication, peristalsis, glandular secretions, hydrolysis and fermentation of food-stuffs, warming of ingesta, cleavage and synthesis during metabolism, and the production of animal heat. All of these have to be provided for before any production can occur, be it growth, meat, milk, or work. The food for internal work is described as the *maintenance ration*;[*] it is the minimum on which the resting animal can be supported without losing body weight and without yielding anything. The amounts of carbon, hydrogen, oxygen, nitrogen, water, and salts entering the body have to be counterbalanced by the amounts of these leaving the body. The *production ration* is that required for growth, or work, or the storing up of flesh, fat, or wool, or the production of milk.

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* If the writer's memory serves him, this period also applied to man during the Great Famine in India many years ago.

† *Veterinarian*, May, 1895.

It is impossible here to give an idea of the enormous amount of work which has been carried out on animals in an endeavour to solve the many problems connected with these questions. Investigations of the chemical composition of food substances, and of the proportion of each digested under various conditions, represent the bulk of the earlier labours extending over half a century. In this way was ascertained the percentage of each food principle digested by various animals, and these discoveries led to a more economical standard of feeding being adopted, but this method of inquiry did not explain the cause of the differences observed. The system adopted in the present day endeavours to get at the root of matters; it utilises the old method of food analyses and the observed digestibility of each food, and then by converting the results into terms of *heat units*—*i.e.*, energy values—endeavours to show what these are capable of contributing to the maintenance of the body or the building up of tissues. The method aims at showing the actual effect of the food on the body, and its content of matter and energy. For instance, under the old system the study of a food, say maize, terminated when its digestibility under various conditions had been ascertained; but by the system of energy values it is possible to go further, and to show with a degree of precision the amount of energy which escapes from the body unused, the amount used up in the work of digestion, the amount used by horses during work, and the amount stored up as fat and protein by the tissues.

Some of the modern appliances used in nutrition experiments on large animals are figured at pp. 359, 361, 363.

The Energy yielded by Foods is ascertained by burning the various food substances in a specially constructed calorimeter in the presence of compressed oxygen, and measuring the amount of heat given off. Every gramme (15·432 grains) of water in the calorimeter raised 1° C. (1·8° F.) in temperature constitutes a *heat unit* or *caloric*. In this way it was shown that:

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[*] Also known as the *basal metabolic figure*.

1 gramme of average protein evolved approximately 5,770 calories, or 5·7 large calories.*

1 gramme of fat evolved approximately 9,300 calories, or 9·3 large calories.

1 gramme of carbohydrate evolved approximately 4,100 calories, or 4·1 large calories.

These constitute physical heat values, and also physiological heat values for fat and carbohydrate; for what is true of the calorimeter is equally true of the body, provided the food is fully metabolised and the end products of carbon dioxide and water are the results of the oxidation.

The heat evolved by protein in the calorimeter is not the heat given off to the body; protein is not fully oxidised, being got rid of as urea and other nitrogenous products, so that not more than two-thirds of its energy is available in the body. One gramme of average protein, according to Rübner, yields only 4·1 large calories in the animal body. It is not the heat evolved which does the work, but the chemical energy contained in the food substances; by the time that the stage of heat has been reached the food has done its work.

It by no means follows that because a food substance has a high chemical energy it is necessarily the most nutritive in the body; this depends on its degree of digestibility. It will be remembered that in the herbivora no food or food principle is wholly digested; there is a residue in the digestive canal which cannot be assimilated, and in consequence passes away as a waste product with the fæces. The amount so lost varies with the particular food employed, and tables of digestibility (for a brief abstract see p. 295 *et seq.*) have been drawn up showing not only the total amount of organic matter assimilable, but also the amount of protein, fat, and carbohydrate in each food substance which is capable of being digested.

The theoretical energy of food is not realised in dietetics, owing not only to the above serious sources of loss, but also to losses due to fermentation, such as that of cellulose, which by becoming converted into marsh-gas and hydrogen is lost to the body. Then there are losses arising from the chemical energy used up in mastication, peristalsis, rumination, cleavage and synthesis of the food substances, none of which results in energy to the body, though all result in heat. There is also a loss as the result of the muscular effort involved in standing. If horses are induced to lie during the day, not only do they rest their limbs and feet, but more of their food is capable of being used for the body requirements; the recumbent position assumed by cattle, sheep, and pigs is of evident value. There are sources of loss resulting from the warming of the ingesta, especially of the water consumed. That this loss of heat is considerable, especially in the winter, may be seen by the shivering from which horses suffer after 'watering'—the result of some gallons of cold water having to be raised to the temperature of the body.

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* See footnote p. 374.

If the tables compiled from Lawes and Gilbert be referred to (pp. 380, 381), we shall obtain illustrations of the following important facts:

1. *No food is wholly digested.* Taking Table I., and selecting oxen as an example, 1,109 pounds of water-free food produced 404·4 pounds of water-free excreta (36·5 per cent.), leaving only 704·6 pounds (63·53 per cent.) metabolised.

2. *The whole of the food metabolised is not stored up.* The cattle in Table I. metabolised 704·6 pounds (63·53 per cent.), but only stored up 68·6 pounds (6·2 per cent.) in the form of dry substance; there was accordingly a deficit of 636 pounds, or 57·33 per cent.

3. *The deficit represents the internal work—i.e., circulation, respiration, mastication, rumination, glandular activity, fermentation, movements of the digestive canal, and heat production.* This amounts in the case of cattle to more than half of the total food substances supplied—to be precise, 57·33 per cent. It is a remarkable fact that the herbivora need at least half of their food exclusively for vital functions and the work of digestion.

4. *The various food nutrients do not undergo equal digestion.* Table V. shows that a little more than 4 per cent. of the protein is digested by cattle and sheep, and from 7·2 to 9·4 per cent. of the fat and carbohydrate matters; the pig obtains much more from his food, but even he can only assimilate 18·5 per cent. of the fat and carbohydrate matter.

We learn, therefore, that there is a great difference between (*a*) the amount of food metabolised, and (*b*) the amount which subsequently finds its way into the tissues or is capable of being utilised by them. The first is described in modern terms as the *metabolised energy*, or that portion of the gross energy of the food which is not lost in the excreta; while the second is called by Armsby the *net energy*, or that part which is capable, after all the previous losses have been deducted, of producing something, be it work, milk, muscle, fat, or wool.

The gross energy of a food is ascertained by burning it in a calorimeter (p. 395); the effect on the system is ascertained by means of the respiration calorimeter (p. 360), which enables food to be traced in the body, and a precise expression of its value in terms of calories to be obtained. Examples of these will be given.

One hundred pounds of the dry matter of timothy hay contain:

Gross energy, as ascertained by the calorimeter	204,940	large calories.
Energy lost by the excreta	120,840	,, ,,
Metabolisable energy	84,100	,, ,,
Metabolisable energy	84,100	,, ,,
Energy lost in the preparation of the food for digestion, etc.	35,470	,, ,,
Net, or productive, energy in 100 pounds of hay	48,630	,, ,,

The net energy is only 23·7 per cent. of that originally existing in the food, and but 57·8 per cent. of the metabolisable energy. The results were obtained with cattle; the figures for the horse are still lower, only 35 per cent. of the metabolisable energy in timothy hay being available.

An example of a metabolisable energy experiment may be quoted from Armsby. The animal was a steer.

Total calories in the ration	29,538
Energy recovered in the excreta, including the gases of fermentation	17,349
Metabolisable energy	12,189

Finally, the method adopted of tracing the nutrients in the body may be stated:

Total calories in the above ration		29,538
In the excreta, including the gases of fermentation and brushings from the skin	17,437	28,930
Heat lost by the body	11,493	
Calories stored up		608

The difference in the amount between the nitrogen and carbon contained in the food and those recovered in the excreta showed that the body had gained 11·1 grammes nitrogen and 46·6 grammes carbon; this was equivalent to 66·6 grammes of protein and 15·2 grammes of fat.

The 66 grammes protein contained	380	calories.
The 15·2 grammes fat contained	144	,,
Total stored up	524	,,

It happens that in this experiment there are 84 calories missing as compared with the calorimeter test, but the principle is unaffected.

These examples give some notion of the laborious nature of nutrition experiments which have been made, or are in course of being made, on all classes of animals and food-stuffs in order to determine with exactitude what becomes of the food in the process of its metabolism. The results form the modern tables employed for calculating the number of calories yielded by food-stuffs to the body.

Tables of food requirements were in the past prepared to show the amount needed during rest, work, or the production of flesh and milk. The physiologist of the present day, while not rejecting these tables, points out that they led people to attach undue importance to the standards, as it appeared obvious that they were being treated as if rigidly exact, though only issued as a guide.

The calories for *maintenance* given below are extracted from Armsby's valuable tables. They embody the work of many observers, and include his own contributions to the subject. He, however, issues a word of warning that the figures should be regarded as the economic rather than as the exact physiological requirements for energy.

MAINTENANCE REQUIREMENTS FOR ANIMALS.

	Digestible Protein.	Energy for Internal Work. Large Calories.	Additional required for Heat. Large Calories.	Total Maintenance Energy. Large Calories.
Horses, body weight per 1,000 lbs. - - -	0·50 lbs.	4,100	7,800	11,900
Cattle (unfattened), body weight per 1,000 lbs. -	0·50 ,,	6,000	4,470	10,470
Sheep, body weight per 100 lbs. - - -	0·055 ,,	790	580	1,370
Pigs, body weight per 100 lbs. - - -	0·048 ,,	1,250	280	1,530

It will be observed that cattle, sheep, and pigs require more energy for internal work than the horse, while horses require more for body heat.

In the above table the 11,900 calories for a horse at rest and not increasing in weight would be furnished by 15 pounds of timothy hay. The researches of Grandeau and Leclerc, carried out on different horses for several months, showed that animals of about 1,000 pounds body weight, doing no work, but receiving half-an-hour's exercise daily, require for their maintenance about 17½ pounds of meadow hay daily, the metabolisable energy of which is equal to 13,000 calories. The total digestible dry organic matter needed was between 7 and 8 pounds daily, irrespective of the composition of the diet, provided the due amount of protein—not less than 0·5 pound daily—was present. The writer kept riding-horses on 12 pounds of hay daily without loss of body weight, the animals doing no work, but the period was much shorter than that employed by Grandeau and Leclerc, whose figures may be adopted for horses in a condition of idleness, though it is to be noted that their animals gained slightly in weight.

Cattle, under the old tables, were allowed for maintenance 0·5 pounds protein and 7 to 8 pounds of non-nitrogenous matter reckoned as starch for 1,000 pounds body weight.

The calories required for production—*i.e.*, for work, flesh, milk, or wool—cannot be dealt with here, as the subject is far too large and falls to the province of hygiene. Nevertheless, a brief statement may be made.

REQUIREMENTS FOR WORK PRODUCTION BY THE HORSE (ARMSBY).

	Digestible Protein.	Net Energy. Large Calories.
Full work (draught) of 8 hours per day -	2·0 lbs.	18,200
Half work (draught) of 4 hours per day -	1·4 ,,	11,100
One-fourth work (draught) of 2 hours per day	1·0 ,,	7,600

These calories cover both maintenance and production. When compared with the maintenance table the figures may appear small, but during work no food is required to be set apart for heat production, as more than sufficient arises from muscular contraction. As a matter of fact, the measurement of work is an extremely difficult matter, and for riding-horses performing natural work at fast paces there seems no probability that even approximately correct figures will ever be available. The revolving platform is valuable for experiments on draught and for the slower paces, but nothing more.

REQUIREMENTS FOR FATTENING (INCLUDING MAINTENANCE).

Cattle per 1,250 pounds weight (average requirements during the whole period), 14,000 calories daily.

Sheep per 100 pounds weight (average requirements during the whole period), 4,000 calories daily.

Pigs per 100 pounds weight (average requirements during the whole period), 4,500 calories daily.

REQUIREMENTS FOR MILK PRODUCTION (INCLUDING MAINTENANCE).

Cows per 1,000 pounds body weight, the milk containing 4 per cent. fat, and the quantity being 20 pounds daily, 11,300 calories.

NET OR PRODUCTIVE ENERGY VALUES PER 100 POUNDS OF SOME FOODS.

Horses :	
Timothy hay	26,640 large calories.
Oats	93,440 ,, ,,
Maize	112,840 ,, ,,
Beans	109,400 ,, ,,
Pigs :	
Barley	106,080 ,, ,,
Maize	118,820 ,, ,,
Bran	74,950 ,, ,,
Potatoes	24,690 ,, ,,
Skimmed milk	14,740 ,, ,,
Cattle and Sheep :	
Timothy hay	32,250 ,, ,,
Red clover hay	43,020 ,, ,,
Oat straw	34,810 ,, ,,
Wheat straw	7,220 ,, ,,
Mangels	5,680 ,, ,,
Maize	85,500 ,, ,,
Oats	67,560 ,, ,,
Brewers' grains (wet)	14,530 ,, ,,
Bran	53,000 ,, ,,

Pathological.

Disorders of nutrition, though much more apparent in some diseases than in others, occur with every departure from the normal condition.

Fever.—The tissues are readily broken down in supplying fuel for the increased metabolism which is giving rise to the abnormally great production and loss of heat; both the fats and proteins suffer, and in some disorders it is remarkable how rapidly wasting occurs the moment the reserve is used up. In acute lung cases this is very obvious—in a fortnight the patient may be a wreck. The increased nitrogenous metabolism which is here indicated suggests an increased excretion of urea, but exact work in this direction is still much needed. During fever there is an increased production of carbon dioxide, and absorption of oxygen; uric acid is formed by the herbivora, and the urine becomes acid.

Marked muscular waste may occur in the absence of fever; anything which causes a drain on the system, such as internal parasites, tuberculosis, internal growths, etc., may reduce the animal to little more than a skeleton. Starving, underfeeding, or overworking of animals are obvious causes of metabolic change; defective teeth in horses are also a frequent cause of malnutrition.

The food supply may be deficient in proteins or carbohydrates, or both, or there may be an excess. Disorders from the latter cause are very evident in the horse. **Lymphangitis** and **hæmoglobinuria** are diseases of the horse intimately associated with overfeeding and idleness, and have no parallel in any other animal. An excess of salts in the food may be productive of considerable trouble. One form of intestinal calculus in the horse is due to the amount of ammonio-magnesium phosphate existing in the bowel through feeding too largely on bran.

Deficiency Diseases have been dealt with in the text.

Broken Wind is referred to at p. 156 as having its origin in errors of dieting and management, such as a bulky and frequently innutritious diet combined with heavy work on a distended stomach and intestines. In view of the new facts stated at p. 156, defective nutrition occupies a less important position than has generally been supposed, and it would appear that under good management, especially during heavy or fast work, the disease should be unknown.

Local loss of nutrition, such as occurs in lameness, is referred to at p. 360.

CHAPTER XII

ANIMAL HEAT

In the chapter on nutrition and elsewhere, the expressions oxidation and combustion, in reference to the food substances and tissues, have been of frequent occurrence. One is tempted to visualise them in likeness of a fire or lamp, and to regard combustion within the body as something very closely akin to, if not identical with, combustions outside the body. A very brief reflection will show that this cannot be the case, for it is obvious that the temperature at which combustion occurs outside the body could not be tolerated by the living organism. Oxidations within the body occur at a relatively low temperature, and, further, the substances contained in the cell are not dry, but are three-fourths water. Again, if oxidation within the body were carried out as oxidations are outside the body, it would be possible to increase tissue oxidation by furnishing the tissues with an increased supply of oxygen. Yet this result is not obtained; the rate of oxidation in the body is not affected either by breathing pure oxygen or by taking in a larger supply of air. Nevertheless, this does not alter the essential facts that the food substances, and in a less degree the body tissues, undergo oxidation, that the source of the oxygen is the air taken into the body, and that this process is continually occurring throughout the whole period of life. It is, therefore, necessary that we should attempt to understand something regarding the processes of tissue oxidation and of how they occur within the living body. It is unfortunate that no positive statement on this question can at present be made, the whole subject being extremely obscure and imperfectly worked out.

Oxidations.—This fundamental fact has already been learned, that the oxidations occurring in the body do not take place in the blood, but in the tissues. By means of oxidations energy is produced, the substances oxidised being protein, fat, and carbohydrate. One form of energy yielded by these on oxidation, and the only one which concerns us in this chapter, is heat.

It may be well, before going further, to observe that there are various forms of energy, but the energy of motion, heat energy, and chemical energy, which are the only sources of supply of energy to the body, are those of most interest in physiology. All forms of energy are convertible into one another, and no loss occurs as the result of conversion; for example, a nail may be hammered to a red heat on the anvil, the energy of motion (kinetic energy) being in this instance converted into heat. Or heat may be a source of kinetic energy, as in the steam-engine; chemical energy may be converted into heat and motion, as in the cylinder of the motor-car, and so on. The heat or work obtained when a unit of one energy is converted into another is always the same; in spite of continual changes in form, energy is neither created nor destroyed.

This great law of the *conservation of energy* applies to the animal body; the potential or stored up energy contained in food is converted into motion and heat energy in the body, and it is possible, as we have seen in the chapter on nutrition, to trace how much escapes as work, how much as heat, and to account with the greatest precision for the total amount received. It has been stated above that all forms of energy are convertible into one another; the second law governing energy deals with the fact that, though other forms of energy may be converted into heat, heat cannot be completely transformed into, say, work, for a part remains as heat. Owing to this incomplete transformation, the losses in the body arising from the production of heat derived from food substances which *have done no mechanical work*, have received detailed consideration in the chapter on nutrition (pp. 393-399); the subject, which concerns the herbivora almost exclusively, is one of extreme importance.

It has been stated above that the process of tissue oxidations is obscure; what is definitely known of the subject is that the free oxygen of the air, when taken into the body, must in some way be changed so as to increase its powers of oxidation. This change, or rather series of changes, is greatly promoted by the presence of ferment-like bodies. If glucose or certain phosphorised fats be exposed to ordinary free oxygen, the oxidation occurring in glucose is so small and so exceedingly slow as to be valueless for the purposes of the body. On the other hand, phosphorised fats and some other fatty substances are acted upon by free oxygen and undergo a process of *autoxidation*, during which process energy is liberated. This energy calls into existence a *peroxide*—namely, an oxide containing an extra atom of oxygen, with consequently a higher power of oxidation than that contained in ordinary oxygen. Peroxide having been formed, the process of oxidation is greatly strengthened, but even the peroxide needs the presence of a body which will increase the rate of chemical reactions. Such a body is known as a *catalyst*, and catalysts act as ferments do, by bringing about changes and yet suffering no loss themselves. Peroxide, plus a catalyst, will oxidise such bodies as glucose and lactic acid into carbon dioxide and water, the necessary catalyst in this connection being the presence of a ferrous salt. Enzymes which furnish catalysts are known as *catalases*. Their function is to liberate gaseous oxygen by decomposing peroxide; they cannot raise the activity of the oxygen. Blood, milk, and most animal and vegetable tissues contain catalases. In living cells, especially in those in the tissues of plants, ferments are found which play the same part as the iron salt above mentioned; they enable peroxide to yield 'active' oxygen, and to oxidise, among other bodies, glucose and lactic acid. These ferments are called *peroxidases*; they contain iron and manganese, which composition appears essential to their working. They are distinguished from catalyses by their ability to raise the oxidising power of peroxide. Peroxidases are found in blood, milk, and other animal tissues. Under the term *oxydases* are included substances found in many tissues, which are a mixture of peroxides and peroxidases; the best known are those acting on phenols (phenol-oxidase), on tryosine (tyrosinase), xanthanase, and uricase.

In the present state of knowledge it is believed that oxidations in the tissues occur through ordinary oxygen having its potential raised to active oxygen, and this is effected by the production of an autoxidisable substance from which is produced a peroxide, which in turn is further activated by means of peroxidase.

The oxidations in the body occur in the cellular elements, and the question arises whether it is the actual living structure of the cells or their fluctuating, and at present unorganised, contents which undergo combustion. It seems quite clear that under the process of normal nutrition the actual wear and tear of the body tissues is relatively small, so that we must look to the floating rather than to the fixed elements as being mainly the seat of oxidations. The protein, fat, and carbohydrate, which, as we have seen, are capable of yielding heat on combustion outside the body, yield an equivalent amount of heat on combustion within the body, excepting that protein, by not being oxidised lower than urea, suffers a loss, one-third of its heat energy being carried off by the urine. We must now inquire as to the behaviour of the heat which is formed in the body.

The Body Temperature.—One important division of the animal kingdom is into warm-blooded and cold-blooded animals. A *poikilothermal*, cold-blooded, or animal of changeable temperature is one in which the body temperature depends upon the external surroundings. When these are cold the bodies of such animals are cold, being about a degree or so higher than the medium in which they are living; when the outside temperature rises, the body temperature correspondingly rises. Such a condition exists in reptiles, fish, etc. A *homoiothermal*, warm-blooded, or animal of practically constant temperature, is one in which the body temperature is independent within wide limits of the temperature of the medium in which it is living; whether this be high or low makes practically no difference. Between these two comes a class partaking of the characteristics of each, *hibernating* animals, which during the summer are homoiothermal, and during the long winter sleep are poikilothermal.

The temperature of the body is not uniform; the interior is warmer than the exterior, and the blood in the interior veins is warmer than that in the corresponding arteries. The blood in the veins leading from a gland in a state of activity has a higher temperature than the blood entering the gland. In the animal body the hottest blood is found in the hepatic veins, while the blood in the posterior vena cava is hotter than that in the anterior. There is also a difference in the temperature of the blood in the right and left hearts; it is generally considered that the blood in the right heart is the warmer, though Colin found that in the horse the blood of the left side was generally the hotter. The brain has also a high temperature. The practical aspect of this question is that the interior of the body is hotter than the exterior. A surface temperature does not indicate the temperature of the body, which for clinical purposes should be taken in the rectum. With the air at freezing-point there may be as much as 3·0° C. (5·4° F.) difference in temperature between the readings in the rectum and on the thin skin of the breast in the horse, while at the same external temperature the limbs of this animal, which are naturally cold, in consequence of the underlying tissues having very little vascularity, may indicate 25·4° C. (44° F.) difference between the temperature of the pasterns and that of the rectum.

The Normal Temperature of Animals.*—Wide differences exist in the normal temperatures of the domestic animals, and marked physiological variation occurs among animals of the same species. In the following statement the temperatures are all rectal or vaginal, and as far as practicable of animals at rest.

Horse: The temperature varies between 100° and 100·5° F. The average obtained by Hobday from a large number of observations was 100·3° F. A temperature of 101° F. is compatible with perfect health, but is exceptional.

Cattle: Robertson found among the fat stock at Smithfield Show an average temperature of 101·6° F.; the temperature of dairy stock was found by Wooldridge† to average 101·4° F., with variations between 100·4° and 102·8° F. Hobday places the temperature of adult cattle at 101·3° F., with a physiological range from 100° to 102° F. Calves have a rather higher temperature than adults, but, in fact, this applies to young animals of all species.

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* These records are very largely based on 'Notes on Physiological Temperatures,' by Professor F. Hobday, *Journal of Comparative Pathology*, vol. ix., No. 4, 1896.

† 'The Temperature of Healthy Dairy Cattle,' Professor Wooldridge, *Proceedings Royal Dublin Society*, vol. x., part iii., 1905.

Sheep: Wide variations compatible with health exist in this animal. Hobday gives the temperature as ranging from 103·4° to 104·4° F., and thinks that 104° F. might be regarded as an average temperature.

Swine: According to Hobday, the temperature of adults ranges from 100° to 102° F., of young pigs from 101·5° to 105·5° F.

Dog and Cat: The average normal temperature is 101·5° F. (Hobday), but the temperature may vary between 101·3° and 102·3° F.

A cause of variation in sheep and swine is the securing of the animal and the overcoming of its resistance to the introduction of the thermometer, but the chief cause of variation in all animals but the horse is the limited power of the skin to get rid rapidly of excesses of heat by sweating. Local temperatures, especially of the limbs and feet in the horse, are frequently ascertained in the routine of practice. Normally, these parts are 'cold' to the sense of touch, but in some forms of lameness they are hot; even warm legs, and especially feet, are pathological. The legs of the horse, it has been said, are cold, owing to the relative non-vascularity of the underlying tissues; on the other hand, the cartilages of the ear have very little vascularity, yet cold ears are pathological. Horn is a bad conductor of heat; the base of the horns in cattle is frequently examined in judging of the presence or absence of fever. The nose of the dog and muzzle of bovines are 'cold' in a state of health, due to evaporation of sweat from these surfaces.

Variations in Body Temperature.—A rise or fall in body temperature does not necessarily imply an increase or diminution in the production of heat. To prove increased heat production it is necessary to show that the metabolism is increased, that more oxygen is absorbed, and more carbonic acid produced. In all animals there is a daily variation in temperature, the lowest records being obtained in the early morning, 2 to 4 a.m., the highest in the evening, 6 to 8 p.m., after which the temperature falls during the night. These variations are due to metabolism; during rest the metabolism sinks, while during activity it rises. The temperature of the young animal is higher than that of the adult, while the temperature of animals in temperate climates living in the open is lower than that of those under cover; in the case of the horse as much as 1° F. difference in temperature has been registered under this condition. In the tropics the temperature of animals exposed in the open, during the day, is higher than that of animals under cover. Other causes of variation in temperature will be considered presently. The thermometer does not tell us the amount of heat formed in the body; it only indicates the resulting difference between the heat produced and the heat lost. These important points must now be studied.

Heat Production.—The oxidations occurring in tissues, and leading to the production of heat, have previously engaged our attention; these changes occur mainly in the skeletal muscles, in which four-fifths of the daily heat are generated, and in active glands such as the liver. The heat furnished by glandular activity is amply demonstrated in the case of the liver, though certainly not in all secreting glands. The temperature of the blood in the hepatic veins is higher than in the portal, higher even than in the aorta. It was shown by Bernard that in the dog, while the portal vein was registering 39·6° C. (103·5° F.), the blood in the hepatic veins was at 41·2° C. (106·3° F.). Heat is formed during muscular contraction. Experiments carried out on the external masseter muscle of the horse showed that during contractions the thermometer registered 2·8° C. (5·0° F.) higher than in the same muscle at rest.

The muscles of the skeleton are not always actively contracting, yet heat is always being furnished by them. The heat produced in muscle not actively contracting is formed as the result of **muscle tonus**—*i.e.*, the stretched condition inherent in muscle, which explains the gaping that occurs when it is cut across. This state of tonus is essential to posture. The simple act of standing demands work from the muscles and evolves heat. The part played by muscle tonus in contributing to the heat of the body is more marked in horses than in cattle and sheep, which lie for long periods during the day. As tonus leads to the absorption of oxygen and excretion of carbon dioxide, the loss of energy due to the standing position may be ascertained experimentally; it has been observed in cattle that the energy generated by muscle tonus in the resting position may be 60 or 70 per cent. of that so generated in the standing position.

As the blood streams out of the muscles its temperature is higher than in the corresponding arteries, and in this way the whole mass of blood would be raised in temperature were it not for mechanisms by which the heat is dissipated. But the excessive production of heat is not always compensated by a sufficiently rapid loss, and a high temperature may in consequence be produced. This is a most important point in connection with working horses. In man a rise of 1° to 1·5° C. in body temperature may occur as the result of work. In the horse half an hour's trotting may raise the temperature from 0·4° to 1·4° C.

(0·7° to 2·7° F.) above the normal; the amount of rise is largely a question of ' condition '; temperatures of 40° to 41° C. (104° to 106·5° F.) after hard work, especially in a hot sun, are not uncommon (Blenkinsop and Hobday). With rest the temperature falls in the course of three or more hours, the mechanism for getting rid of heat being able to act; as heavy a fall as 4° F. in two hours has been recorded (Willis). In animals unfit for work owing to want of condition the temperature may take longer to fall, or even remain above the normal sufficiently long to be designated febrile; ' fatigue fever ' is not unknown in man. If the handling of animals produces excitement or struggling, the temperature will rise.

The act of feeding, which involves increased muscular activity, not only immediately, but subsequently in the muscles of the whole alimentary canal, slightly raises the temperature of the body. In the horse, according to Siedamgrotzky, the temperature as the result of feeding may rise 0·2° to 0·8° C. (0·4° to 1·4° F.); but, according to this observer, there is no similar rise in the ox; on the other hand, Wooldridge found a rise of 0·3° F. in dairy cattle. That heat is formed during the masticatory processes we have already seen from the observations on the masseter muscles of the horse; but the mechanisms for regulating heat in the body are such that a rise of anything like 1·4° F. as the result of feeding must be regarded as exceptional.

We shall see presently that in the herbivora a large amount of heat is generated in the body in consequence of the ' work of digestion,' but this is used up in cold weather in warming the body, and in warm weather is an excretion. The intake of food increases the heat production in all animals, protein by stimulating metabolism being particularly effective in this respect; but in the herbivora there is, in addition, a heat production due to the fermentative character of the food. This source of heat is negligible in carnivora, more important in omnivora, but most important in herbivora. An increased production of heat does not necessarily entail a higher body temperature; if more is formed, more is got rid of.

Influence of the Nervous System on Heat Production.—Heat production in muscles is under the control of the nervous system; impulses transmitted through the motor nerves, and thus giving rise to chemical changes in the muscles, result in the formation of heat. These impulses mainly originate in the skin, and by their means heat is produced according to requirements. If an animal be poisoned with curare, the motor end-plates are paralysed; in consequence, less heat is formed in the muscles, and the temperature sinks; in fact, the animal becomes for the time being practically cold-blooded, the body temperature rising and falling with the surrounding temperature. The same condition may be produced by dividing the spinal cord in the neck, by which means the motor nerves are cut off from the muscles, and the animal becomes practically cold-blooded. In chloroform narcosis heat production is also greatly disturbed; in prolonged operations this should be borne in mind, and the loss of heat guarded against. Shivering is a physiological process associated with the production of heat to compensate for a loss. A hibernating animal, on waking up, shivers, and thus rapidly raises its temperature. The shivering which occurs in horses after being ' watered ' is caused by the consumed water abstracting heat from the tissues in order that its temperature may be raised to that of the body. The ' freshness ' of a horse on a winter's morning is the outcome of nervous impulses instinctively started with the object of generating more heat in the body.

Heat Centres.—It is evident that the mechanism for the production and loss of heat must be under the influence of some nerve centre. A heat centre has been located in the *corpus striatum*, and this is activated by the temperature of the blood circulating through it. If the blood be raised in temperature, the body mechanisms for producing loss of heat are stimulated, the bloodvessels dilating, particularly those of the skin. If the centre be cooled, vaso-constriction results. The removal of the cerebral hemispheres and thalamus reduces the animal to a permanently ' cold-blooded ' condition, though life may be maintained for some time—in the pigeon from one to three months—by keeping the animal in an incubator at 30° C. (86° F.).

Experimental injury to the corpus striatum, the so-called '*heat puncture*,' causes an increased production of heat, which may last for some time without, apparently, causing the animal any inconvenience. It is supposed by some that this experiment does not necessarily prove the existence of a heat centre, the effect of the puncture being to produce a more rapid conversion of liver and muscle glycogen into glucose, the increased temperature being due to the increased combustion of sugar. Others regard the rise in temperature as being due to stimulation of the vaso-constrictor centre in the medulla.

Heat Loss.—Unless some arrangements existed in the body for the regulation of the temperature, the heat resulting from metabolic activity would continue to rise steadily until it accomplished the destruction of the animal. In order to maintain the temperature at a constant point, heat production and heat loss must balance. This balance may be struck either by heat production being diminished, or by increased loss of heat. The temperature of the body may rise either in consequence of an actual increase in metabolism, or through difficulties in getting rid of heat. The process by which, within narrow limits, accurate and prompt adjustment is made is known as **heat regulation,** or **thermotaxis.**

Physical and Chemical Regulation.—The conditions influencing the regulation of the body temperature are grouped into physical and chemical. By *physical regulation* are understood the changes occurring in the temperature and humidity of the air, evaporation from the skin and mouth, losses by radiation and conduction, and those occurring as the result of the food and water consumed being raised to the body temperature. The nervous mechanism involved in these processes consists of the vasomotor nerves to the skin, the sweat nerves, and the respiratory centre. By *chemical regulation* is understood the maintenance of body temperature by metabolism, the nervous mechanism being the motor nerve supply to the muscles, while the fuel is furnished by the food. The thyroid and adrenal glands are believed to participate in the mechanism of chemical regulation, for the thyroid stimulates the secretion of adrenalin, which by increasing the discharge of liver glycogen leads to increased heat production. Adrenalin in sufficient quantity may also diminish heat production by causing constriction of the vessels of the skin.

These two regulations work in conjunction, and that the utmost nicety exists in their interrelationship is shown by the relatively slight changes in the daily temperature at all hours and at all seasons of the year. We must look at this system of regulation in greater detail.

If cold water be poured on a hot body, the body is cooled; if the surface of a heated body be wetted and the water allowed to evaporate, the body is cooled. If a cold body be placed in contact with one which is hot, heat is lost. And processes somewhat similar to these are occurring in the animal body.

1. By *radiation and conduction* heat is lost to surrounding bodies, provided, of course, that they are at a lower temperature than that of the animal; if the surrounding medium is hotter than the animal's body, then heat is gained instead of being lost, so that radiation is of little importance in very hot climates. The natural or artificial covering, be it hair, wool, or clothing, checks the loss by radiation and conduction, as in a dry condition these are bad conductors of heat. When wet, however, they are good conductors, and a considerable amount of heat is lost by sweating or rain. Clothing acts by imprisoning an amount of warm air, the air so confined being a bad conductor of heat on account of its being still.

2. By *evaporation* from the skin the sweat is converted into vapour and heat is lost, the rapidity of the process depending on the humidity of the air and its rate of movement. If the

air be saturated, no evaporation occurs from the skin, and, consequently, no heat is lost. The value of evaporation as a source of heat-loss in the horse is considerable, probably higher than the figure fixed for man—viz., 14·5 per cent. of the total—but no exact information is available. Evaporation is constantly occurring; the sweat, when the amount is small, is evaporated as fast as it is produced, and this is termed in the chapter on the skin 'insensible perspiration.' The sensible perspiration is that which is not evaporated as rapidly as it is produced, and is the source of the most effective loss of heat.

3. *Evaporation from the mouth and nostrils, warming of inspired air, and vapourising of water from the lungs.* The former is a very valuable means of heat loss in those animals which do not sweat from the general surface of the skin; the moist nose and open mouth of the dog are good examples of the working of the principle, and in a much smaller degree the bedewed muzzle of the ox. The warmnig of the inspired air and the vapourising of water from the lungs are most important sources of heat loss in those animals which sweat imperfectly. The panting respirations of the dog, and of cattle and sheep in 'show' condition, are simply a means of cooling the body by warming a larger volume of air, and offering a moist surface for evaporation. All animals in hot countries breathe more rapidly during the heat of the day.

4. *By the urine and fæces* a loss of heat is incurred through the food and water having been warmed to the temperature of the body, though in both these cases there is no actual loss of heat until they are excreted as urine and fæces. The amount of loss thus brought about must be relatively considerable, especially in winter; the abstraction of heat after drinking may be so great as to cause shivering; observation shows that drinking a pailful of water at 50° F. may cause the body temperature of the horse to fall 0·5° to 0·9° F. A diet of 'roots,' containing 80 per cent. water, is a heavy source of heat loss with cattle in winter.

The heat lost by conduction, radiation, and evaporation, is greater in small than in large animals, as small animals have a relatively larger surface exposed in proportion to their body weight (see Fig. 114). A dog of 66 pounds weight will lose 79·5 per cent. of his body heat by radiation and conduction, and 20·5 per cent. by the evaporation of water; whereas a dog weighing 8 pounds will lose 91 per cent. by radiation, etc., and 9 per cent. by water evaporation.

Bulk of body is a safeguard in large animals against sudden loss of heat, and all warm-blooded animals living in the sea are bulky. It takes considerable heat-loss to lower the body temperature of a bulky animal such as the horse; conversely, small animals, in which, as we have seen, the cooling surface is relatively greater than in large animals, must be able to increase rapidly their heat production.

The skin as a source of loss of heat is largely controlled by the nervous system. Through the vasomotor nerves the vessels are constricted or dilated; when the vessels are constricted, the skin becomes pale (though this may not be seen, owing to hair and pigment) and the blood is thrown upon the internal viscera, where it is additionally shielded from loss. In consequence, the skin becomes cold and the loss of heat less, not merely as the result of the lessened radiation, but also and chiefly as the outcome of the diminished evaporation. When the vessels are dilated the skin becomes flushed and hot, the veins stand out with blood, and a large amount of heat is lost. This vasomotor action is an automatic reflex act, as also is the nervous control over the sweat glands, by which more or less water is poured out on the surface of the body and heat lost by its evaporation. This nervous control is normally set in action by changes in the temperature of the surroundings.

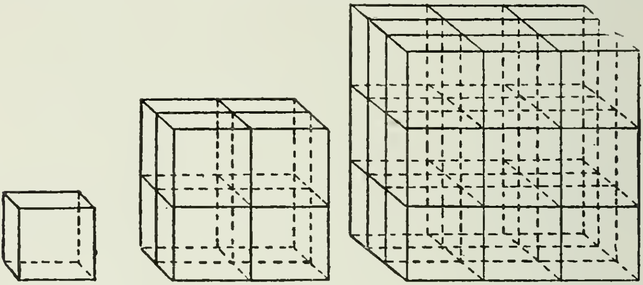

Fig. 114.—Diagram to illustrate the Relation between Volume or Weight and Surface (Waller).

The volumes are 1, 8, 27 cubic centimetres.
The weights are 1, 8, 27 grammes.
The surfaces are 6, 24, 54 square centimetres.

That is to say, their ratio of increase is 1, 4, 9.

The loss of heat is influenced by the thickness of the natural covering, its colour, etc. That from a rabbit after shaving off the fur is one and a half times greater than before shaving. A sheep before shearing excretes less carbon dioxide and more water than the same sheep after shearing. White rabbits lose 75 per cent. of the heat lost by black or grey, for white not only absorbs less heat during the day, but loses less heat at night. Grey horses are better suited to the tropics than horses of any other colour, and black horses least of all. The black skin of the negro protects the deeper tissues from the sun's rays, from which it might be argued that black horses in theory should stand exposure to a tropical sun better than grey; but a grey horse has a black skin, and the pigment prevents the rays from penetrating. Loss of heat from the body surface can be experimentally produced by varnishing the skin, and the animal then dies from cold unless wrapped up in cotton-wool (see p. 324).

Influence of Heat and Cold.—A moderate degree of cold applied to the external surface of the body increases the production of heat, due to increased oxidations. This results, as we have seen, from reflex impulses discharged through the motor nerves. At the same time, in man, the appetite is increased to meet the extra demand, and foods rich in fat are instinctively sought for. This principle should be observed in the feeding of animals, and an increase allowed in the food to meet the extra oxidations, fat, if possible, forming part of it. The body will stand a considerable degree of cold, but a point may be reached where the rate of heat production is below that of heat loss, and the animal dies from cold. Conversely, the body is adjusted to withstand a moderately high external temperature; the heat of Arabia or India, which renders surrounding objects, such as metal, too hot to hold, and causes the very birds to sit with drooping wings and wide-open mouths, is borne with impunity by the acclimatised horse; the heat-regulating mechanisms do not allow the external heat to be stored up. A continuous rise in external temperature cannot be long borne, and a point is reached at which the heat kills; for when the discharge of heat from the body ceases, as it does when the surrounding air goes above a certain point, heat becomes stored up, and heat-stroke follows. A far higher temperature can be borne when the air is dry than when it is moist, as evaporation from the surface practically ceases in a moist atmosphere. Men have been exposed to a temperature of 127° C. (260° F.) for a few minutes without ill effects, and with no elevation of the body temperature. When air has its humidity increased by 1 per cent. the loss by radiation and conduction is raised 32 per cent., while an increase of 25 per cent. in the humidity of the air is equal to an increase of 2° C. in the external air. At a temperature of 31° C. (88° F.) in an atmosphere saturated with vapour the regulating mechanism of man is exhausted, and a rise in body temperature occurs. Horses taken from cold to hot latitudes have to learn to compensate, and until they do so a febrile rise in body temperature, with increased respirations and pulse, will occur as the result of standing in a hot sun, even though doing no work. This passes away with acclimatisation, but increased respirations on a hot day are always evident even in animals of the country.

The loss of body heat by animals lying out at night is partly prevented by the fatty covering to the peritoneal cavity, which prevents undue conduction of heat. Wet, combined with exposure, causes a more important loss of heat than mere cold. It has been shown from exact observations on man that a limb clothed in wet flannel lost 34·4 per cent. more heat than the same limb in dry flannel. Animals never look so wretchedly miserable as after a night of cold rain; under the conditions of active service, a cold, wet night is certain to kill off the most debilitated.

A physiological resistance to cold can be obtained by training; the body learns to regulate its loss and production of heat, and this brings us to a consideration of the interesting practical point of the necessity of clothing for animals, especially for horses, in a state of domestication. Some animals, such as the horse, ox, and sheep, are born fully developed and clothed; in a few minutes they pass from a temperature of between 101° to 105° F. within the womb of the parent to perhaps freezing-point on the bare ground. The power of regulating their temperature is fully established, and in a very short time this is assisted by muscular movements of the limbs, which are learnt very quickly; the gambols of young animals serve some other purpose than that of expressing mere lightness of heart. Cold has no effect on these young creatures, if healthy, provided the parent is able to supply sufficient nourishment. There are other animals, such as pups, kittens, rabbits, and certain birds, such as pigeons, which are born blind, helpless, and more or less naked; they cannot move, are unable to regulate their temperature, and if taken from the maternal warmth, their body temperature steadily declines and they die from cold. In these the capacity for regulating body temperature does not develop for some little time after birth, and until locomotion becomes possible.

Effect of Low Temperatures.—We have seen, then, that the horse comes into the world prepared by its heat-regulating mechanism to accommodate its body to the external temperature. In due course this is supplemented by an extra growth of hair for winter use and a lighter covering for the summer. If no interference with the coat be practised, it is undoubted that no artificial covering of any kind is required during the coldest weather, and even where the natural covering is of the lightest, as with the thoroughbred horse, it is sufficient for its purpose. The thoroughbred brood mares of this country, once they go to the stud, live in the open for the remainder of their lives, and never wear a blanket. And practical experience teaches us that this condition may be gradually imposed on all horses with impunity, even on those which have been kept in hot stables. Coughs, colds, and inflammatory chest affections, usually attributed to cold, are practically unknown among horses living in the open, even during the coldest weather, and it is easy to show that these diseases are largely the result of the artificial conditions under which working horses have to live.

Jackson* has proved that the law of adaptability which applies to men living in the Polar regions applies with equal force to horses; for two and a half years he kept horses at 80° north latitude. During this time the thermometer never rose higher than 11° F. above freezing, while 70° to 80° F. below freezing were common temperatures. During the sleighing expeditions these animals lived in the open, and wore one blanket, which, as may be seen in Fig. 115, found its way where most blankets get, under the hind-feet. At the time the photograph was taken the animals were in a temperature of 45° F. *below zero* at night—viz., as far below freezing-point as summer heat is above it. It is interesting to note they did not suffer, and Major Jackson informs the writer they were never frost-bitten, and never had a cough or cold. Exposure to a low temperature renders the body sensitive to a rise in the thermometer. Jackson tells us that the July temperature of 8° above freezing-point made it feel like midsummer, and far too warm! Conversely, living in a high temperature renders the body very sensitive to a fall in the thermometer.

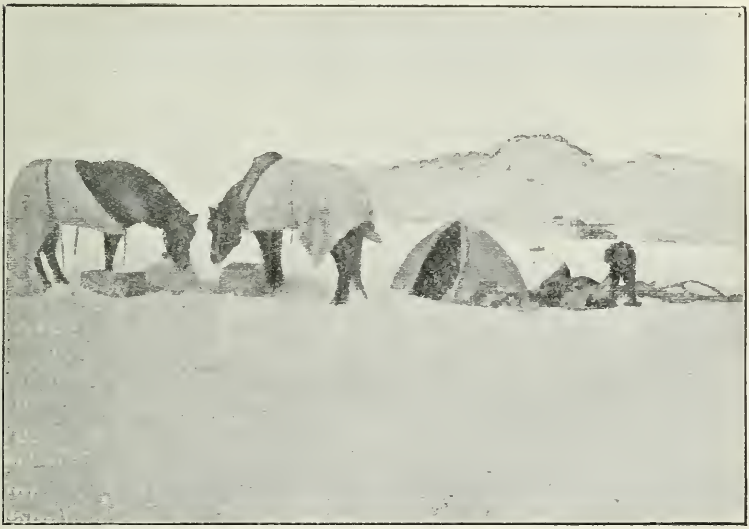

FIG. 115.—PONIES LIVING IN THE OPEN IN THE ARCTIC CIRCLE AT 45° F. BELOW ZERO (JACKSON).

If a part be persistently protected against air-currents, it becomes sensitive to exposure; if it be habitually exposed, a considerable degree of cold can be borne with impunity. Our faces are never covered, and the hands by some only. People who wear no gloves do not complain of cold hands, and it takes a winter of Arctic intensity to make the face feel cold. Women commonly wear far less clothing than men, and in consequence, under the necessities of fashion, they exhibit a remarkable degree of tolerance to cold. The bare-footed child is not conscious of cold feet, nor is he, nor the hatless man, marked out as a subject for catarrh. We have the evidence of Darwin* that unclothed man can withstand the most tempestuous climate in the world outside the Arctic Circle. The natives of Tierra del Fuego at the time of Darwin's visit wore nothing; newly-born infants were exposed like their parents. These people did not die from cold, in spite of the rigours of the climate; their heat-regulating mechanisms were evidently perfect.

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* 'A Thousand Days in the Arctic,' F. G. Jackson.

Clipping.—Now that the clipping of horses can be done expeditiously and cheaply, fashion decrees that the horse shall be clipped all over. There is no necessity to remove the whole of the hair of the body; for working horses limited clipping is all that is required, and when this is done they do not feel the effects of being robbed of their natural cover, even though no clothing be supplied. After twenty-four hours they do not feel the cold any more than a man does who has had his hair closely cut; nevertheless, they are losing, in consequence, more heat, and therefore require more food. It is economical to clothe the horse which is wholly clipped. Siedamgrotzky observed the effect of clipping on the temperature of horses. He found that the temperature rose after the operation, and fell to normal about the fifth day. It was observed that clipped horses had during exercise a higher rectal temperature by 1·8° F. than unclipped horses, and the return to normal was more steady and regular with them than with unclipped. The rise in temperature after clipping may be due to vasomotor action; less blood being in the skin, more will find its way to the viscera—viz., to parts of the body which have a naturally high temperature, the result being that the total mass of blood will have its temperature raised. Another way of accounting for the rise in temperature after clipping is by supposing that an actual increase in the production of heat occurs; this may be due to stimulation of the skin influencing the heat production in the muscles.

Hibernation.—The effect of a fall in the temperature of the bodies of animals is to produce a depression of metabolism. This is well seen in some mammals—such as the dormouse—which sleep all the winter, during which time they live upon the store of fat laid up in the tissues during the summer. Owing to their depressed metabolism this store is found sufficient to keep them alive, though they wake up at the end of the winter mere skeletons. On their waking up shivering occurs, and the body temperature rises by bounds to the normal, the animal then returning to the condition of an ordinary warm-blooded animal until the recurrence of the next period of hibernation. As to the causes of this remarkable phenomenon we know but little. It is not confined to only one class of animals, since it occurs in mammals, amphibians, reptiles, etc. No purely anatomical differences suffice to explain why some animals hibernate and others do not. External cold is usually assumed offhand to be the initiating factor, assisted possibly by the lessened food supply at the approach of winter. But some other more recondite cause than either of these must exist, since marmots may sometimes hibernate in the summer, and dormice will hibernate even if kept warm in the winter; cold will not necessarily cause an animal to hibernate except at the appropriate season, and *severe* cold may even arouse a hibernating animal from its state of torpor.

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* 'Voyages of the *Adventurer* and *Beagle*.'

Critical Temperature.—When an animal is fasting, as, for instance, in the experiments made to determine the katabolism of the body (see p. 366), the temperature remains constant, being maintained by the metabolism incidental to the *internal work of the body* (p. 395), there being a minimum consumption of the fat, glycogen, and protein of the tissues. In addition, there is heat produced from muscle tissues due to the necessary muscular effort connected with standing. As the animal is kept as far as practicable absolutely still, the heat formed in the body during fasting is a measure of the internal work, and experimental inquiry shows that this quantity of heat is approximately the same from day to day. The amount of heat determined in this way fixes the amount of the *maintenance* ration (pp. 393, 398).

During a fasting experiment there is a favourable air temperature in which the amount of heat produced in the body is exactly counterbalanced by the amount lost. This favourable air temperature is known as the *critical temperature.* Above the critical temperature there is heat to the good, which is got rid of by the ordinary means of physical regulation; on the other hand, below the critical temperature heat is being lost faster than it is being made. It is a mistake to suppose that with every fall in air temperature there is a call for more heat supply. It is not until the critical temperature is reached that the heat production of the animal is at a minimum; below the critical temperature there is a call for more heat, and this is furnished by chemical regulation. Conversely, by raising the external temperature no effect is produced on the quantity of heat produced by the body as the result of its expenditure of energy, for the energy required for the internal work is approximately constant.

The critical temperature has not been determined for all animals: for the dog it is about 20° C. (68° F.); for the guinea-pig, 30° to 35° C. (86° to 95° F.); for the pig, 20° to 30° C. (68° to 73° F.); for cattle, no definite temperature has been fixed (Armsby, from his experiments, regards it as rather low); for man, wearing ordinary clothes, it appears to be about 15° C. (59° F.).

If a fasting animal be placed on a *maintenance* ration, the air temperature being above the critical point, the effect of the food is to cause an increased production of heat which lasts some hours. The cause of this is the mechanical work involved in mastication, the passage of the material along the digestive tract, the glandular activity excited, the stimulating effect on metabolism produced by the food elements, especially protein, and in the herbivora the fermentations arising mainly from the digestion of cellulose. To these Armsby adds, as the result of his experiments, a variety of undefined substances in the food of the herbivora which stimulate tissue metabolism. The heat arising in this way has been termed 'the work of digestion.' The whole of the heat formed as above is not the outcome of vital functions, that resulting from the fermentation of cellulose is, if we may so describe it, heat to the good, for though the cellulose is largely, if not entirely, lost to the body as nutriment, the heat resulting from its fermentation remains, and as the critical temperature approaches, instead of being got rid of as an excretion, is used to warm the body. The consequence of this is to lower the critical temperature, and the more liberal the feeding the lower it falls. In the case of the horse 100 grammes of digested crude fibre and other carbohydrates produce 69·7 large calories due to fermentation, and in ruminants 60 calories. All this is available for body heat when the air temperature falls. The advantage of this to the herbivora is considerable, and explains why, when well fed, they are able to stand cold and exposure with impunity; the heat arising from the fermentation of the cellulose and other carbohydrate material, instead of being got rid of is utilised to warm the body, and by so doing it conserves the chemical regulation and lowers the point at which combustion of the tissues has to make good the loss due to cold. This explains the common mistake of regarding the feelings of herbivora and our feelings to cold as being identical. It cannot be too distinctly stated that if animals are well fed they can withstand practically any degree of cold and exposure without suffering in health. Hot stables, cattle-sheds, and cow-houses are a fruitful source of disease; yet the prejudice against cool surroundings is widely spread; it is largely based on our own subjective feelings to cold, which, as we have shown, are not identical with those of animals.

The **Amount of Heat produced** by animals depends upon the rate of their metabolism and the surface area of their bodies; the latter factor determines the loss of heat, and hence its production if the temperature of the body is to be kept constant. A large animal produces actually, but not relatively, more heat than a small one; a small animal, as has been previously stated, has a greater body surface relative to its weight than a large animal, and in this way its loss is greater. As heat production must balance heat loss, the small animal must relatively lose more heat, and therefore produce more heat, than the large animal.

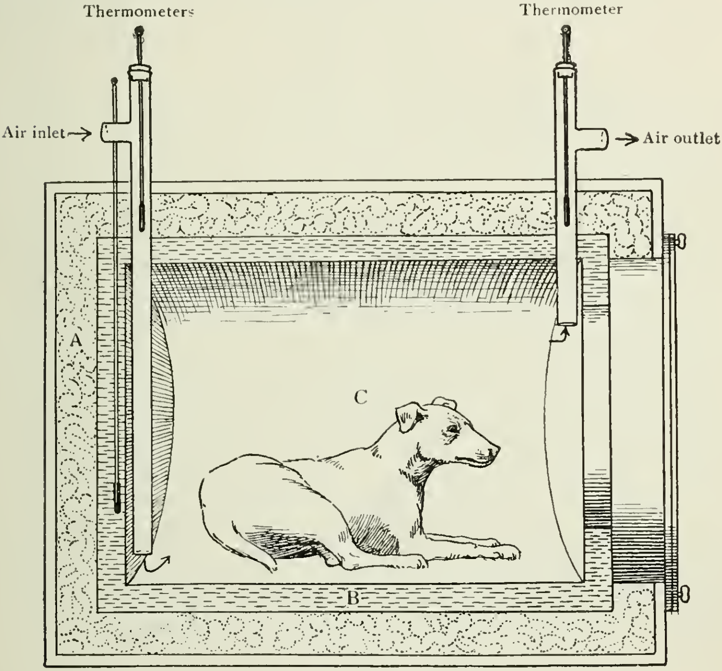

FIG. 116.—CALORIMETER.

The animal is resting in the chamber, which has a double wall containing water, There is an air inlet and outlet to the chamber, and delicate thermometers for ascertaining the temperature of the water, and of the incoming and outgoing air. The whole is placed within another chamber and surrounded by packing of non-conducting material.

A, Outer insulating chamber; B, middle water-chamber; C, inner chamber.

The heat produced is measured as heat-units or calories—viz., the amount of heat required to raise 1 gramme of water 1° C., known as the *small calorie*, or the amount required to raise 1 kilogramme of water 1° C., which is the *large calorie*, sometimes spoken of as the 'kilo-calorie.'

The method by which the heat given off by a body is ascertained is by means of a **calorimeter** (Fig. 116). This is a chamber with a double wall containing air or water, which absorbs the heat given off, say, from an animal in the chamber. This chamber is contained within another, and the two are separated by non-conducting material in order to prevent loss of heat by radiation. The weight of the water in the calorimeter is known, and the extent to which its temperature is raised during the experiment ascertained; a simple calculation shows the number of calories given off during the observation. The temperature of the animal's body before and after the experiment shows whether the loss of heat has been made good or not, or whether, on the contrary, the body has produced more heat than it got rid of. By the process of calorimetry the heat value of food is also ascertained. In the respiration calorimeter described at p. 360 the heat given off from the body is compared with the heat contained in the food, and the energy expenditure ascertained.

In the present state of our knowledge it is not possible to state with anything like precision the number of calories required by animals for maintenance or production. The figures as they stand at present have been given in the chapter on Nutrition (pp. 398, 399).

When the amount of heat produced daily by animals during fasting is compared with the area of the body, a close agreement is found between various animals of different sizes. The explanation is that already given at p. 411; the large animal produces more heat than the small, owing to its greater katabolism, but the relatively larger surface and more intense katabolism of the small animal eliminate the difference due to size. It has been stated that the body surfaces of animals of geometrically similar figures are proportional to the two-thirds power of their weights, and on this basis calculations of body surface for cattle and a few for horses have been made; but as Armsby properly points out, young and old, and fat and thin animals are not geometrically similar. The following table, however, which gives the number of large calories produced in 24 hours per square metre of surface, shows that the results obtained with some animals closely approximate:

	Number of Large Calories.
Man	1,042
Dog	1,036
Pig	1,045
Mouse	1,188

The figures for cattle and horses are not reproduced, as they are too doubtful, while those calculated for the sheep by Armsby show that this animal does not obey the law. The metabolism of sheep per unit of surface is little more than 60 per cent. that of cattle. This is not apparent from the table given at p. 398, but is evident when the metabolism of the two animals is compared to the body surface. Armsby suggests that in the sheep the thick coating of wool tends to reduce the amount of heat lost, so that in the process of evolution the intensity of metabolism and the intensity of heat emission in this animal have undergone mutual adjustment.

Post-mortem Rises of Temperatures are frequently observed, and some of the observed temperatures have been remarkably high. The writer recorded in the horse 109° F. between the liver and diaphragm. The explanation is that metabolism is still occurring in some of the tissues, but since there is no circulation to carry the heat away the temperature of the part rises.

Pàthological

The actual processes occurring in fever are not known. It cannot be definitely stated whether the increase in temperature is due to an increased production of heat or to a disturbance of the mechanism by which the loss of heat is regulated—probably both causes are in operation. It has been supposed by some that fever may be due to the action of bacterial poisons on the heat-centres, and it has been stated that cultures which produce fever in the intact animal no longer do so on division of the pons, which cuts off the basal ganglia heat-centre from the rest of the body. Others have considered that, though the nervous mechanism is at fault in some cases, in others the heat-forming tissues themselves are at fault, being too active. This view receives some support from the action of agents employed in the treatment of fever; whereas some, like quinine, act on the tissues, others, like antipyrin, appear to produce their effects through the nervous system, particularly by their action on the vessels of the skin. Fever leads to a marked increase in the metabolism of protein. This is shown by an increase in the output of nitrogen; uric acid appears in the herbivora; ammonium salts of organic acids and creatinine are increased, and creatine, which normally does not appear in the urine, may now be found. The absolute amount of urea is greater than normal, but its proportion to the other urinary nitrogenous substances may be relatively less. Fever is probably a beneficial mechanism in infective processes by assisting in the destruction of bacteria and their products; nevertheless, high temperatures effect great damage to the body-tissues, especially to the heart-muscle, and methods which control temperature appear clinically to give the best results in treatment.

CHAPTER XIII

THE MUSCULAR SYSTEM

THE muscular system is the largest in the body, the skeletal muscles alone representing 45 per cent. of the body weight.

The regulation of the blood-supply, the movements of the skeleton, the contraction of the heart, and the transport of the ingesta along the intestinal canal, are all examples of muscular movement, and, further, they are examples of different kinds of movement; the slowly moving muscle of the intestinal canal is very different from the active skeletal muscles, and these, with their long periods of activity and rest, are in great contrast to the rhythmical movements of the heart muscle.

Structure of Muscle.—There are three varieties of muscle in the body:

1. Voluntary, skeletal, striped, or red muscle.
2. Involuntary, pale, smooth, or unstriped muscle.
3. Heart muscle.

The *voluntary muscles* exist generally in large masses known as 'flesh,' and their function is to move the skeleton. The muscle mass consists of bundles, the bundles are composed of smaller bundles, the smaller bundles are made up of fibres. The *fibre* of a muscle does not run the length of the bundle; on the other hand, a primitive fibre is only about 4 or 5 centimetres ($1\frac{1}{2}$ to 2 inches) in length, and of microscopic thickness—viz., $\frac{1}{500}$ inch on an average. The fibre is as a rule unbranched, its ends are rounded, and it is enclosed within a sheath, or *sarcolemma*. Each fibre is made up of bundles of minute *fibrils* or *sarcostyles* embedded in a semi-fluid contractile substance known as *sarcoplasm*. The fibrils constitute the contractile substance of the fibre; they show markings which produce the transversely striated appearance characteristic of red muscle, and are composed of *sarcous elements* or *sarcomeres*, minute bodies of peculiar structure placed end to end in the fibril like beads on a string.

In some muscles, such as those of the heart and diaphragm, the sarcoplasm exists in relatively large amounts; such muscles are deeper in colour than ordinary skeletal muscle; they contract more slowly, and may be said never to tire. Striped muscle may therefore be dark as in the case of the heart, full tinted as in the ordinary skeletal muscles of the larger herbivora, or a pale bloodless-looking structure, such as is found in the rabbit and some fishes. In the rabbit both pale and red fibres may be mixed up in the one muscle. These pale striated muscles exhibit structural differences from ordinary striated muscle.

The *nerve* supply to voluntary muscle is both motor and sensory: through the *sensory nerves* the brain is made acquainted with the posture of the body and the condition of muscular tension. This implies the existence of a special **muscle sense,** which plays such an important part in locomotion. In the muscles this sense is served by special bodies generally found near tendons, called *neuro-muscular spindles;* these are from $\frac{1}{8}$ to $\frac{1}{3}$ inch in length, and $\frac{1}{125}$ inch in width; each spindle is of muscle surrounded by a sheath, and has a sensory nerve entering it at one end. Nervous structures, known as the *tendon organs of Golgi,* also exist in the tendons at their junction with the muscle fibres; they consist of spindle-like bodies connected with one or more fine, medullated nerve fibres. These nerves are in communication with the portion of the brain which is devoted to 'muscle sense.' The ordinary degree of sensibility in muscle is not very great unless the part be cramped or inflamed, though pain is caused when they are cut into. By means of the *motor nerves* the muscle is supplied with impulses which, originating in the brain, passing thence along the spinal cord, and emerging by the ventral roots, finally reach the skeletal muscle concerned, and bring about contraction. Division of the motor nerves, or interference with their function, causes paralysis of the muscle or muscles supplied by them. Each motor nerve enters the primitive fibre about its centre, and terminates in a special organ known as an *end-plate.* By means of *curari* this end-plate may be paralysed, in which case stimulation of the nerve leads to no muscular response in consequence of the block, though the muscle itself remains irritable, and readily responds to direct stimulation.

The question of the nerve supply to muscles will receive fuller consideration when the subject of 'muscle sense' is dealt with in the chapter on the senses (Section IV.). It will also engage attention in the chapter on the Nervous System, when the extremely important subject of *reflex inhibition* is discussed. It will suffice here to point out that the nerves conveying impulses which pass from muscles, which later on will be known as *afferents,* are numerous, while the nerves conveying impulses which pass to muscles, known as *efferents,* are fewer and are limited in function to the transmission of those impulses which stimulate contraction.

There is no set of efferents to a voluntary red muscle which prevents or controls contraction, though obviously this is as important as the initiation of it by excitatory impulses. How this difficulty is overcome is a matter for future consideration.

Masses of material of the structure outlined above are intended for the transport of the body, for which purpose they are united to the skeleton either by tendons or by the direct insertion of their own fibres. In the muscles of the limbs, and wherever, in fact, the parts are exposed to great strain, the tendon insertion is the most usual. There are certain muscles in the machine on which the strain is so considerable that tendinous material is intimately mixed up with the muscular tissue; this is well seen in the masseters, the muscles of the back, forearm, and thigh. The muscles of the limbs, back, and abdomen are also supported by a bandage in the form of fasciæ; this is thick and elastic over the abdomen, fibrous around the limbs, and of great strength. The fascia of the thigh of the horse frequently maintains in position the ends of an undisplaced fracture of the tibia, sometimes for days, and even under the influence of work in draught! That of the arm is not so powerful.

During progression the muscular strain is enormous; for example, in the canter and gallop a weight equivalent to that of the whole body is propelled by one fore-leg (see chapter on locomotion). In the horse provision is made for the muscles of the limbs being rested without necessitating the animal assuming a recumbent position; this mechanism will be explained when we come to deal with the locomotor system; by means of it an animal can sleep standing, and may remain standing for some weeks without serious suffering.

Involuntary, or Pale Muscle, is not found in masses as is the red, but in thin sheets, which in places, such as the bloodvessels, are only of microscopic thickness. Pale muscle is employed throughout the whole length of the digestive canal from the stomach to the rectum; it is also found in the bladder, uterus, spleen, bloodvessels, and elsewhere. In none of these places is the sharp, short, active contraction of skeletal muscle required; slow, steady, deliberate movements are essential in the digestive canal; slow, steady, expulsive movements are necessary in the bladder and uterus, and even in the bloodvessels, where, as we have seen, the muscular tissue acts like a tap, it is sufficient if this tap is turned on and off slowly and steadily.

In structure pale muscle consists of nucleated, longitudinally striated, spindle-shaped cells, dovetailed and held together by a cementing substance; it is through the medium of this substance that the wave of excitation passes from cell to cell, in which respect pale muscle forms a great contrast to voluntary muscle, where, as we shall see, the whole contracts, not by the spread of the stimulus from one fibre to another, but as the result of all the fibres being stimulated simultaneously. There are nerves and ganglion-cells in abundance in pale muscle; the nerves, which are chiefly non-medullated, form a fine plexus with the ganglion-cells, which are placed at the junctions of the plexus. It is probably due to these cells that involuntary muscle continues to contract when all connections with the centre are destroyed, though some physiologists see reason for thinking that the contraction of pale muscle may be carried out just like that of heart muscle—namely, as a self-acting mechanism, independent of any nervous connections.

The nerve supply of involuntary muscle is peculiar, and presents a great contrast to that of red muscle; whereas the latter receives only one variety of motor supply, pale muscle receives two, there being one set of fibres which *stimulates* contraction, and another which *inhibits* it. Both sources are derived from the sympathetic system.

Heart Muscle, as we have seen (p. 33), is in structure both red and striated; nevertheless it is involuntary; the fibres are characterised by being formed of branched, nucleated, quadrilateral cells, while the sarcolemma is absent. We have also seen that heart muscle possesses automatic action and a double nerve supply which increases and decreases its activity. In these respects it closely resembles pale muscle. In common with all varieties of muscle it possesses tonus (see pp. 407, 434); its fibres may be stretched by the dilatation of the cavities of the heart without the stretching producing increased tension on the heart's contents, as is the case with other hollow organs—for example, the bladder. The increased length of fibre thus obtained gives rise, as in voluntary muscle, to a contraction of greater energy.

Muscular Contraction.—This apparently simple act is extremely complex, and will require to be dealt with in some little detail.

Muscles are tissues possessed of **irritability** and **contractility**—viz., they possess the power of responding by a movement to the application of a stimulus. The normal stimulus is effected through the motor nerves under the control of the brain or spinal cord, but of the nature of this stimulus we are ignorant. A coarse reproduction of it can be effected by pinching, pricking, chemical, thermal, or electrical stimuli, applied to either the nerve or the muscle itself, and to all these the three varieties of muscle are responsive. When a muscle contracts, the energy set free is directly proportional to the length of its fibres immediately before they begin to contract. As the result of contraction there is no change in the volume of a muscle, but it becomes shorter and thicker; it undergoes changes in its extensibility, elasticity, and temperature; there are also alterations in its electrical condition and chemical composition, and a greatly increased flow of blood through it.

Most of the information which has been gained regarding muscular contraction has been ascertained by employing the muscles of the frog, which retain their irritability for a long time after removal from the body. Such a muscle suitably prepared is known as a *nerve-muscle preparation,* and with certain modifications what is found to occur in this as the result of contraction occurs also in the living mammalian muscle.

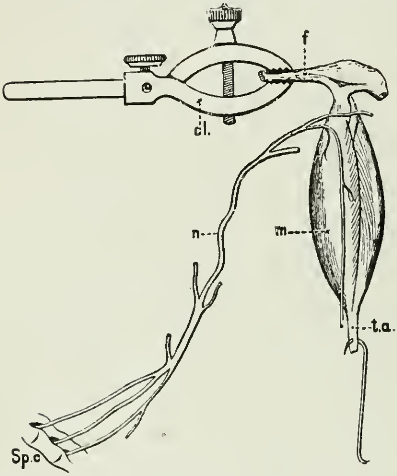

Fig. 117.—A Nerve-Muscle Preparation (Foster).

m, The *gastrocnemius* muscle of a frog; *n*, the *sciatic* nerve dissected out back to *Sp. c*, the lower end of the spinal canal; *f*, femur; *cl*, clamp; *t a*, *tendo Achillis* with **S**-hook attached for carrying a weight.

The muscle most usually and conveniently employed for investigating the phenomena of muscular contraction is the *gastrocnemius* of a frog, dissected out in such a way as to leave its upper tendon connected with a piece of the femur and its lower tendon, the *tendo Achillis*, intact though free. At the same time care is taken not to sever the connection of the muscle with its motor nerve, the *sciatic*, which is dissected out for some considerable distance back towards its point of exit from the spinal canal, the central end being, if desired, left connected to a portion of the spinal cord enclosed in a piece of the lower end of the spinal column. The muscle is then suspended by fixing the remains of the femur in a clamp; a small **S**-hook is attached to the tendo Achillis. This muscle-nerve preparation and its arrangement as above described is shown in Fig. 117.

For purposes of experiment the preparation is fixed inside a small chamber with glass sides to prevent the drying of the muscle and nerve; this is effected by placing a few pieces of wet filter-paper inside the chamber. The sciatic nerve is laid over a pair of electrodes connected by wires to binding-screws outside the chamber; by this means any desired electrical stimulus may be applied to the nerve. A thread attached to the hook in the tendo Achillis passes through a hole in the floor of the moist chamber, and is connected with a horizontal lever free to move in a vertical plane, a small weight being hung under the lever to give the muscle the 'load' necessary for its efficient contraction. The free end of the lever is then brought to bear against the vertical surface of some recording apparatus—usually a cylindrical drum covered with smoked paper—made to rotate by clockwork about a vertical axis.

An inspection of Fig. 118 shows at once that if the drum of the recording instrument rotates, the end of the lever connected to the muscle must trace out a horizontal line on the smoked surface. If the drum is stationary and the muscle is made to contract, the

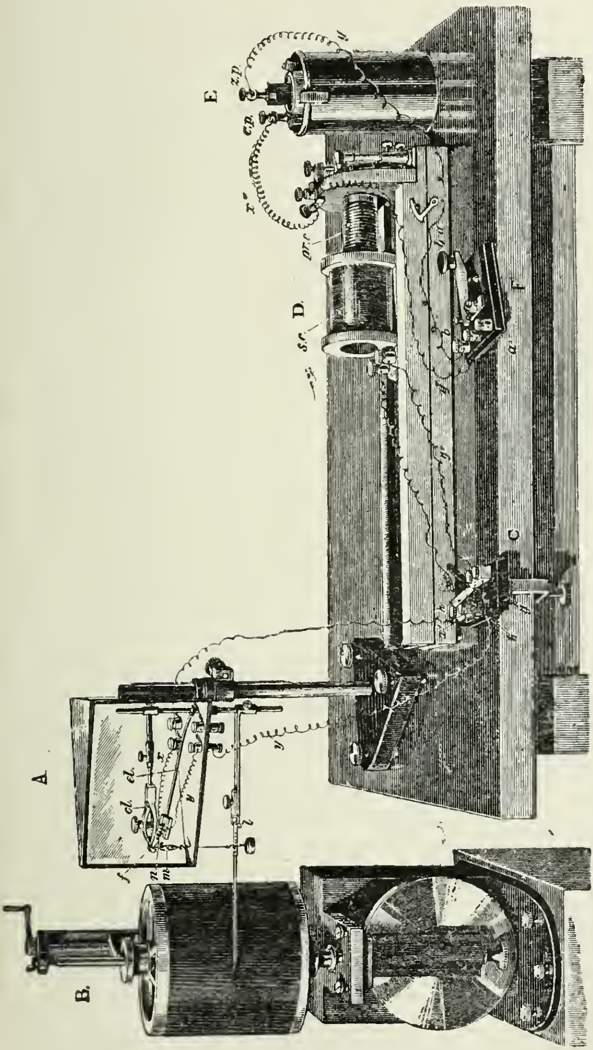

Fig. 118.—Diagram showing a Typical Arrangement of Apparatus and Instruments for Experiments with a Nerve-Muscle Preparation (Foster).

A, The moist chamber; *m*, muscle; *n*, nerve; *f*, femur; *cl*, clamp. The nerve is shown laid over the end of the electrode-holder *el*, connected by the wires *x y* to the outside of the chamber; *l*, the lever with which the muscle is connected by a thread and S-hooks; B, rotating drum, carrying the smoked paper on which the lever makes its tracing; C, a key for controlling the connection of the electrodes in the moist chamber with the secondary circuit *s c* of the induction-coil D; F, a key for making or breaking the connection of the battery-cell E with *pr c*, the primary circuit of the induction-coil D.

lever will trace a vertical line. If now the muscle is made to contract while the drum is rotating, a curve is traced of which the ordinates of the various points and the general shape give us exact information as to the details of the contraction from start to finish.

The electrical currents employed in stimulating muscles to contraction are of two kinds—the galvanic or constant current, and the induced or interrupted current.

The *galvanic current* is conveniently supplied by a Daniell's cell, (E, Fig. 118), in which zinc is the positive and copper the negative element. These metals are connected with wires to the poles or electrodes. The electrode attached to the zinc element is not however, the positive, but the negative, or *kathode*, pole, and, similarly, the electrode attached to the copper is the positive, or *anode*, pole. Within the battery the current flows from zinc to copper outside the battery—viz., between the poles it flows from copper to zinc. The circuit is completed by bringing the poles together, known as 'making'; it is broken by separating the poles, known as 'breaking.' When this current is passed through a galvanometer—an instrument which detects the existence, direction, and intensity of currents—it flows through this apparatus from the positive to the negative pole. So much confusion results from the use of the terms 'positive' and 'negative'—which, as we have seen, have two opposite meanings, depending upon whether the current is passing through the battery or through the poles—that Waller has proposed that physiologists should call the copper 'galvanometrically positive,' and the zinc 'galvanometrically negative,' in the same way that physicists employ the terms 'electro-positive' and 'electro-negative' to indicate the positive and negative elements respectively.

The *induced* or *interrupted current* is produced by passing a galvanic current through an induction-coil (D, Fig. 118). This consists of a primary coil, *pr c*, connected with the Daniell's cell, E, and a secondary coil, *sc* D, capable of a sliding adjustment near to or away from the primary coil. The nearer the coils are together, the stronger the current. To the secondary coil wires are attached conveying the induced current. Between the battery and the primary coil is introduced an appliance for making or breaking the current. This may be done by hand, when single shocks are required, by means of the key F, Fig. 118, or automatically by means of an interrupter, when a rapid succession of make and break shocks are required. This interrupter may be seen in Fig. 118 to the right of the standard supporting the primary coil.

The most conveniently controllable stimulus for experimental purposes is that of single induction currents or the interrupted current of an induction-coil. These have the advantages of being extremely efficient as stimuli, and of giving rise in the nerve to impulses which may be regarded as the nearest artificial approach to the impulses which in the body are discharged along the nerves by the cells of the central nervous system.

If by means of a myograph (Fig. 119) a tracing of a muscle contraction is made on a revolving drum, a muscle curve is produced. A **muscle curve** consists of three parts: (1) A period following stimulation during which no contraction occurs; it is known as the *latent period*, and during this time the muscle is preparing itself for work; (2) a period of *contraction* or shortening; (3) a period of *relaxation* (see Fig. 119).

The length of time involved in the various phases of a contraction may be measured by bringing a time-recorder, vibrating fractions of a second, to bear on the smoked surface of the revolving drum; the sinuous line in Fig. 119 below the muscle curve is produced in this way. Though the nerve was stimulated at the point marked 1 on the tracing, it was not until 2 was reached that the muscle responded, the time value for the latent period being $\frac{1}{100}$ second. As a matter of fact, the latent period is less than this, for a very slight loss in time occurs in the impulse passing along the nerve, and there are also instrumental defects, such as friction of the lever, to be allowed for. When these allowances are made, the latent period is reduced to about $\frac{1}{250}$ second. The entire contraction from the instant of stimulation to the end of relaxation occupies about $\frac{1}{10}$ second.

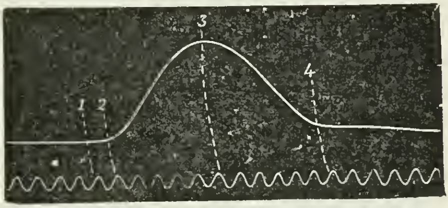

Fig. 119.—The Curve from a Single Contraction of the Gastrocnemius Muscle of the Frog (Waller).

From 1 to 2 is the latent period; from 2 to 3 the period of shortening; from 3 to 4 the period of relaxation. The sinuous line below the curve indicates periods of $\frac{1}{100}$ second.

The latent period, contraction and relaxation of a muscle are affected by certain conditions. It is found that *with increase in the weight* a muscle may be called upon to lift, the shorter the contraction and the longer the latent period. If we continue to weight the muscle a point is reached when it is unable to lift the load. With an *increase in the strength of the stimulus* there is, up to a certain point, increased contraction, and also a shorter latent period; beyond this point, known as a 'maximal stimulus,' an increased stimulus produces no effect.

If a fresh preparation be kept contracting and recording its movements it will be observed that as the muscle settles to work the first few contractions successively improve, each being stronger than the preceding. This progression is known as the *beneficial effects of contraction*, and the character of the record is described as 'staircase' (see Fig. 120). The contractions then become less, the latent period, the period of contraction, and especially that of relaxation, become longer as the muscle approaches the condition of *fatigue*. This may be seen in Fig. 121, where the muscle has been made to contract at the same point at each revolution of the drum.

If the muscle be now left to itself it will recover, though on restimulation it is more easily fatigued than before

The *effect of heat* on a muscle preparation may, in very general terms, be stated as follows: Moderate warmth increases the height of the contraction and diminishes the latent period and length of the curve. Cold decreases the height of the contractions. Very low temperatures cause the muscle to lose its irritability. A high temperature, 42° C. (107° F.), produces heat rigor and kills the muscle by coagulation of its plasma.

A practical demonstration of the destructive influence of a high temperature on heart muscle is afforded by pneumonia. Horses may be killed by this disease in the course of forty-eight hours, at a time when ample area for ventilation remains in the lungs. The sodden parboiled appearance of the heart muscle tells its own story.

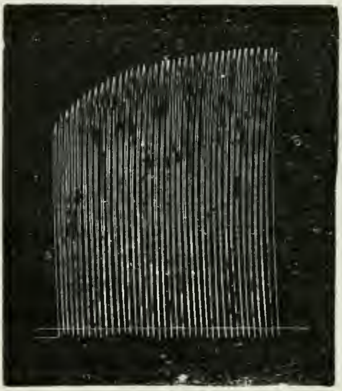

FIG. 120.—'STAIRCASE' CONTRACTIONS OF SKELETAL MUSCLE: FROG (STEWART).

The *effect of veratrine poisoning* on muscular contraction is very remarkable; apart from the fact that the curve sometimes shows a second contraction, there is a prolonged period of retarded relaxation or maintained contraction (see Fig. 122).

Summation.—If instead of a single stimulus being passed into a nerve-muscle preparation two are sent in, so timed that the second follows the first before the muscle has time to relax from the first contraction, the contraction due to the second stimulus is superposed on the first, and the effect obtained is a stronger total contraction. If a third stimulus be sent in before relaxation occurs from the second, the lever of the muscle preparation will describe a curve still higher than the preceding, and so on, until a maximum is reached when it can go no higher. Such a piling up of contraction on contraction is known as *summation of contractions* (Fig. 124).

Tetanus.—If an induction current be applied to a muscle or its nerve, a rapid succession of stimuli is thus introduced, and there is no time for complete relaxation to occur between each successive stimulus. This may be seen in the lowest curve of Fig. 124, in which ten stimuli per second were passed into the muscle, and partial relaxation only will be observed to have occurred between each of them. In the middle curve twenty stimuli per second were used, and the amount of relaxation is represented by a slightly wavy line; in the upmost curve thirty stimuli per second were employed, and the curve shows

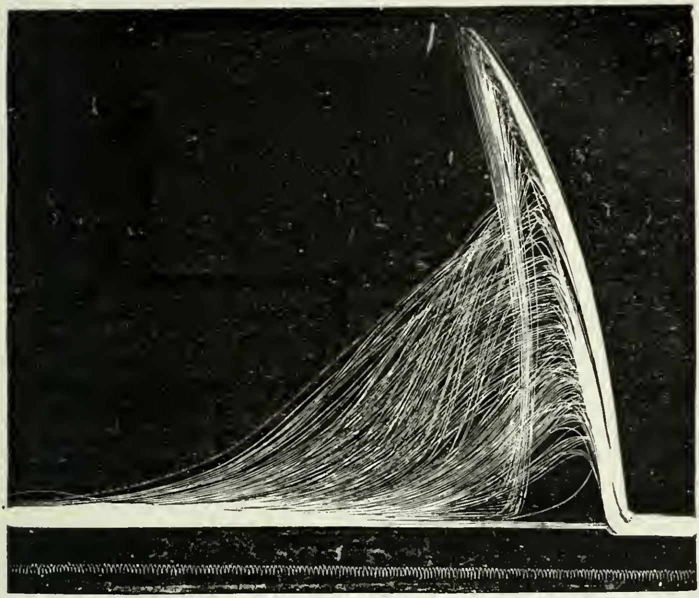

Fig. 121.—Fatigue Curve of Skeletal Muscle: Gastrocnemius of Frog (Stewart).

Time-tracing $\frac{1}{100}$ of a second. The curve is read from right to left.

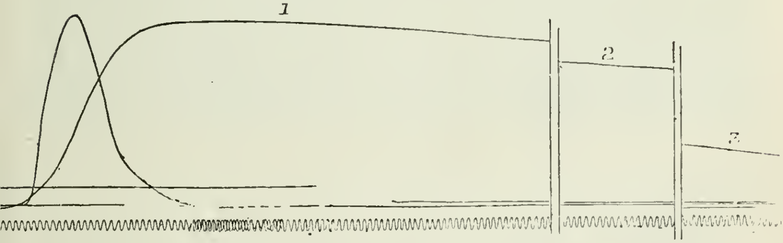

Fig. 122.—Veratrine Curve compared with Normal: Frog's Gastrocnemius (Stewart).

The tuning-fork marks hundredths of a second. Between 1 and 2 a portion of the time-tracing corresponding to one and a half seconds has been cut out, and between 2 and 3 a portion corresponding to one second. The veratrine curve does not show a peak. At 3 it has not yet fallen to the base-line.

no relaxation; the muscle is in the condition of *tetanus*. Tetanus, therefore, consists of a series of short contractions with an insufficient interval for intervening relaxation.* The number of stimuli per second required to provoke tetanus depends on the condition of the muscle, the nature of the muscle, and the class of animal; for example, in the bird, 100 stimuli per second; in the tortoise, 3 stimuli per second; in the rabbit, 20 to 40 stimuli per second for the pale voluntary muscles, 10 to 20 for the red muscles. In insects, whose muscles can contract a million times

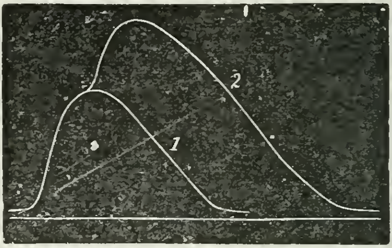

FIG. 123.—SUPERPOSITION OF CONTRACTIONS (STEWART).

1 is the curve of contraction due to the first stimulation; 2 is the curve of the second contraction, superadded to 1 by applying the second stimulus at the moment when the first contraction had nearly reached its maximum.

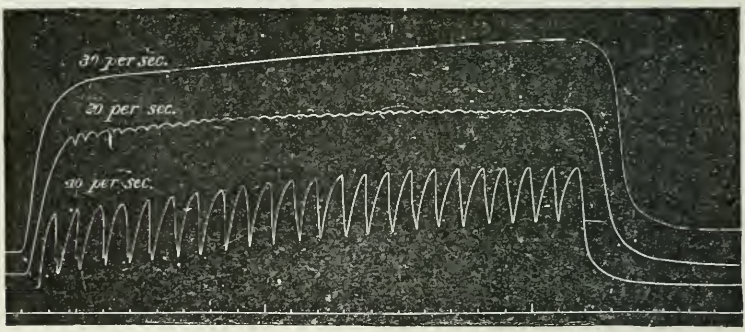

FIG. 124.—SUMMATION CURVES OF MUSCLE CONTRACTION (WALLER).

The lowest curve is one obtained by stimulating the muscle ten times every second; the intervals of relaxation are clearly seen, though there is a slight summation shown by the slanting rise of the tracing. In the middle curve the shocks were twenty per second, and the relaxation is only of a very partial kind. The upmost curve is that of tetanus.

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* The tetanus of the physiologist must not be confused with the tetanus of the pathologist; the latter is a bacterial affection producing a poison which causes painful contraction of many of the voluntary muscles of the body, especially of the limbs and jaws.

an hour, 300 stimuli per second are required to produce tetanus. A fatigued muscle is more readily tetanised than one which is fresh. All the voluntary muscular contractions of the body are regarded as tetanic in nature—namely, as a series resulting from a succession of impulses passed into the muscle so rapidly that there is no interval for relaxation.

Phenomena of Contraction: Smooth Muscle.—Though there is a marked difference in appearance of red and smooth muscle, the actual phenomenon of contraction does not differ excepting in the matter of rate. The latent period, the contraction and relaxation are present, but occur slowly and deliberately; smooth muscle may be completely isolated from all nervous connections and still continue to exhibit spontaneous contractions. At p. 424 have been noted the various regions where this type of muscle is found; that of the digestive tract in a recently killed animal is readily available for study, and the eye may easily follow the whole phenomenon of muscular contraction, as the intestines continue to move spontaneously for some little time after death. Mechanical stimulation, such as a tap or pinch, excites a sluggish but marked response of peristalsis, which begins at the precise spot stimulated; even drawing the finger lightly over the stomach wall may produce ‘ weals ’ of contraction, though the stomach is less likely to exhibit spontaneous contraction than the intestine.

When stimulated by a continuous or induced current, the muscle responds in the same way as red muscle, but from 100 to 500 times more slowly; summation also is present, though this is not identical in character with that observed in red muscle, for no contraction follows the first three or four stimuli; the stimuli accumulate before producing their effect, and subsequent stimuli produce an increased height of contraction. Tetanus may also be produced in smooth muscle.

Muscle Wave.—When the impulse enters a muscle at the middle of each fibre, the part nearest the end-plate contracts first, and the impulse spreads each way to the end of the fibre; this process is so rapid, the fibre being only, as we have seen, about 1 inch in length, that for all practical purposes the whole muscle contracts at one and the same time. When, however, the nerve-endings in a muscle are paralysed by curari, the part becomes at once practically nerveless, and if under these conditions one end of the muscle be stimulated, a wave of contraction passes along it to the other at a rate of about 3 to 4 metres (10 or 12 feet) a second in the curarised muscle of the cold-blooded frog. In the muscles of warm-blooded man, where the metabolic processes are more active than in the frog, the rate of progression is greater, and may be taken as 10 to 13 metres (30 to 40 feet) per second. The time which the wave takes to pass any one point of the muscle is extremely short, $\frac{1}{10}$ second; and if (in frog's muscle) we take its velocity as at least 10 feet per second, it may be shown, by means of suitable apparatus, that the *length* of the wave is about 1 foot (30 centimetres). This is a fact of great interest in connection with the efficiency of muscle as a machine. It insures that each single fibre of which the skeletal muscle is composed, and hence the whole muscle itself, can be placed in a state of complete contraction from end to end at the same moment.

Fibrillar Contraction.—The skeletal muscles, when exposed immediately after death, show irregular contractions, bundles of muscle fibre contracting and relaxing irregularly, producing a flickering, quivering appearance. This is known as *fibrillar contraction,* and, as we have already seen, it becomes a serious pathological condition when it affects the heart muscle.

Elasticity and Extensibility.—Elasticity is the property a body possesses of returning to its shape after stretching; extensibility is the power a material possesses of stretching. A piece of steel is elastic, a piece of putty is extensible. If a steel spring or a piece of elastic be tested by loading them with weights, the stretching is proportional to the weight employed; but if a muscle be gradually weighted, it is found that the greatest degree of extension occurs at the beginning, and as the load is increased the extensibility becomes less. Living muscle is very extensible, and is also elastic. It is therefore stretched by a slight force, and returns to its original length when the extending power is removed.

Muscle Antagonism.—Every muscle or group of muscles possesses an antagonist, and though the antagonist may be equal in size, this is not always the case (*cf.* the mass of the muscles which close the jaws and the trifling size of those which open them). Muscle antagonism insures a smoothness of working not otherwise obtainable, as the muscles, in contracting, are working against an elastic resistance. When the flexor of the metatarsus of the horse is ruptured, the effect of the absence of antagonistic resistance is well demonstrated; the gastrocnemii muscles, owing to the absence of antagonism, jerk the leg behind the body, and in this position the skin covering the cap of the hock is thrown into folds, while the Achilles tendon is kinked and flaccid.

Tonus.—Muscle tonus has already received a brief notice in the chapter dealing with Animal Heat, its definition being stated as the condition of tension, or stretching, of muscles, even of muscles apparently at rest, which causes them to gape when they are cut across. As a matter of fact, the expression 'tonus' has not been employed in the same sense by all physiologists. Sherrington says it is the most misused term in physiology.

This authority places tonus on a new plane.* He reminds us that the function of muscle in producing movement is so striking that we are liable to overlook the equally important fact that it also maintains *posture*. In maintaining posture the muscles are not producing movement, but they are functioning statically.

There are numerous postures: standing, sitting, crouching, gazing, and such-like; there are also the postures assumed in grazing, in scratching, and even in rearing; the closed sphincters are, in reality, only instances of postural contraction, whether affecting the digestive tube, the bladder, or the pupil of the eye. Nor is tonus (posture) limited to the skeletal muscles; it affects heart and bloodvessels as well as the plain muscle of the viscera.

The act of standing is due to tonus of the extensor muscles of the fore and hind limbs, combined with tonus of the muscles which bend the spine upwards, and of those which retract the head and neck and lift the tail. The muscles antagonistic to these—namely, those which do not counteract the effect of gravity—are the flexors of the limbs and the depressors of the spine and tail. These antagonistic muscles are not endowed with tonicity.

One of the most striking experiments in physiology is that devised by Sherrington, in which an animal, deprived of the whole of its brain excepting the medulla and pons, is found to be able to stand in the upright position, even for several days, and under appropriate stimulation to rest its limbs or employ them as in locomotion. This is evidence of the reflex character of 'posture,' a subject which will engage our attention in the chapter on the nervous system; nevertheless, it is necessary here to make it clear that tonus of the muscles which maintain the body in the upright position exists only so long as the nerves running from the muscles to the nerve centres are intact; if these be divided, tonus, and consequently posture, is lost.

It is important that we should possess a clear physiological understanding of the method by which, for example, a horse is able to stand for weeks—sometimes, indeed, for years—as a consequence of impulses, not necessarily under the control of the will, passing from the 'standing' (extensor) muscles to the central nervous system. Such knowledge may help us to appreciate some of the pathological features associated with an inability to maintain the upright position either as the result of disease or injury. The act of standing will be further referred to in the chapter dealing with Locomotion.

An animal at rest does not maintain the position of 'attention' indefinitely; for example, a horse standing idle rests his hind-limbs alternately; rarely, unless on apprehension of trouble, does he stand with both hind-feet squarely together or both on the ground. This alternate flexion of the hind-limbs indicates the presence of another mechanism in connection with posture; the extensor muscles which have been keeping the limb rigid have yielded to the flexors, but not entirely so, or the limb would double up; the extensors are still acting; they have lost none of their ability for maintaining the body upright, but they have become *longer* than they were originally; in the words of Sherrington, they have assumed 'a new postural length'; a 'lengthening reaction' has been brought about, and with it, remarkable to say, practically no departure from the muscle's previous state of tonus. Conversely, the extensor muscles may shorten, in which case a 'shortening reaction' has been produced, though still without any increase in the tension of the muscle. It is by means of the lengthening and shortening reactions of the extensor muscles that the 'latitude of pose' is permitted in all animals at their convenience, without a forward or backward step being made. As Sherrington says, 'we are so accustomed to regard the muscle fibre as an elastic string that this property of exhibiting different lengths, while exhibiting one and the same degree of tension, appears contrary to our fundamental notions of muscular activity.'

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* 'Postural Activity of Muscle and Nerve,' *Brain*, vol. xxxviii., part iii., 1915, from which this section has been compiled.

The contracted condition of the muscles which produce posture is relatively unfatiguable; the decerebrated cat may stand for days. It is supposed that the economy with which posture may be maintained is due to some difference between the chemico-physical process of postural, as compared with ordinary, muscular contraction. It has been suggested that there are fibres in muscle specially told off, as it were, for postural work. According to another view, the sarcostyles are the contractile elements of the muscle, the sarcoplasm being the postural elements; it is probable that these two elements in muscle are under different sources of innervation, cerebro-spinal nerves supplying the sarcostyles, while the sympathetic supplies the sarcoplasm. The metabolism which occurs in contracting muscles originates in the katabolism of carbohydrate substances; on the other hand, in muscle tonus it is probable that the nitrogenous substances are broken down.

It has been shown that the labyrinth of the internal ear and nerve-endings in the tendons and muscles of the neck are concerned with the reflex adjustment of the head, eyeballs, jaws, and limbs; if the neck be flexed after destruction of the labyrinths, there is a decreased contraction of the extensor muscles of the fore-limbs and an increased contraction of those of the hind-limbs; extension of the neck dorsally increases the contraction of the extensor muscles of the fore-legs, and decreases that of the extensors of the hind-limbs. If the head be twisted to one side, the limbs of that side to which it is turned exhibit increased extension contraction; those on the opposite side of the body show decreased extension contraction.

The lengthening and shortening reactions described above are of peculiar interest in connection with the pale muscle of the hollow viscera. Both the stomach and bladder can alter in capacity without altering the tension of their muscular walls. They are capable of assuming a capacity (posture) suited to the volume of the contents without material increase in tension, from which it is evident that the muscular fibres lengthen or shorten to accommodate the contents, and do not behave as would a rubber bag under similar conditions. 'The living bladder, unlike the dead bladder or rubber bag, enfolds its contents with the same light grip, whether these contents be ample or little.' The length of the abdominal muscles exhibited by a 'tucked up' horse and a mare in advanced gestation, are other examples of lengthening and shortening reactions.

Muscle Work.—A muscle is capable of vigorous or slow contraction, or of any degree of action between these extremes. When it is energetically contracting, all its fibres are employed; when gently contracting, a few fibres only are at work. The explanation is that it is impossible for the nerves to introduce varying strengths of stimulation. There is only one degree of stimulation capable of transmission, so that each fibre has to work at its greatest effort, the all-or-none feature referred to at p. 53 in dealing with the heart muscle. By reducing the number of fibres in action any degree of slowness of contraction of skeletal muscle is obtained. If a muscle preparation be loaded with successively greater weights, it is found that up to a certain maximum the load actually increases the amount of work done by the muscles. This is due to the influence of the *tension* exercised on the fibres, by which they are increased in length and thereby rendered more vigorous; they meet the increased resistance by an increased effort, as we have already seen in the case of the heart muscle. By our continuing to increase the weight, a point is reached when the muscle preparation becomes overloaded, and in consequence shortens less. These facts are illustrated in the following table:

Load in Grammes.	Lift in Millimetres.	Work done in Gramme-Millimetres—viz., the Load Multiplied by the Height.
5	27·60	138·00
15	25·10	376·50
25	11·45	286·25
35	6·30	220·50

The table also shows that when the muscle shortened the least it lifted its greatest weight. It is obvious that if a muscle lifts no weight it does no work, and its energy goes off wholly as heat. Experience shows that there is a load which varies in different animals of the same species, according to the *quality** of their muscles, from which the greatest proportion of effective work can be obtained. Finally, there is a load just in excess of the strength of the muscle known as *the absolute power of the muscle.* This has led to a paradox associated with the name of Weber—namely, that a contracting muscle may have the same length as one uncontracted. Yet we are all familiar with the fact that this is so; a horse called upon to draw a greater weight than he can move is employing strongly contracting muscles, but they become no shorter; he does no effective work, but his muscles liberate heat, and this is what occurs in the condition known as 'tonus.' In the chapter dealing with Locomotion the important practical questions of the effort a horse can exercise in draught and the weight he can carry are discussed.

If the weight of the load and the height to which it is lifted be known, the work done by a muscle is readily calculated. Work equals the load lifted multiplied by the height through which it is raised, and may be expressed as pounds or tons lifted 1 foot, or grammes or kilogrammes lifted 1 metre.† In the case of animals, the work is expressed as pounds or kilogrammes per foot or per metre of horizontal transport. The amount of work produced by muscles may be calculated in terms of heat. One small calorie =426·5 gramme-metres of work (426·5 grammes raised 1 metre high). Muscular work may also be calculated from the amount of oxygen absorbed: 1 c.c. of oxygen consumed =2·07 kilogrammetres of work.

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* Robertson points out that in the race-horse the difference between a 'stayer' and a 'non-stayer' lies in the relative proportion which the pale bear to the dark red fibres in muscle. In the stayer the dark red fibres greatly predominate ('The Principles of Heredity applied to the Race-Horse,' J. B. Robertson, M.R.Ç.V.S.).

There is a wide difference in the quality of muscles of individuals; they differ as greatly as mental characteristics, to which they bear some relation. Slowness of speech and physical slowness are, as we might suppose, frequently associated, the laryngeal muscles being as slowly responsive as the skeletal. Precisely the same conditions are met with in animals; there is the keen excitable horse, bursting to 'get away,' restraint merely increasing resistance, in contrast to which there is the 'slug,' on which neither encouragement nor punishment has anything more than a temporary effect. Even where temperament, 'condition,' and physical development are apparently identical, there are great differences in the muscular effort, as shown by the *rapidity* of contraction. This is seen in the prize-ring as well as on the race-course, and constitutes what has, for want of a better name, been spoken of above as *quality*. The quality of a muscle may be due to a structural difference of either muscle or nerve, or both, but it is intimately connected with the effectiveness of the circulatory mechanisms.

† A 'horse-power,' the unit used in engineering, equals 33,000 foot pounds of work *per minute*.

The **ergograph** is an instrument employed for recording voluntary muscular contraction in man; it is shown in Fig. 125. The person experimented upon lifts a known weight to a definite height, which is recorded on a drum. Each contraction is followed by the same interval of rest. Observations with this instrument show that after complete fatigue at least two hours are required for the muscle to recover sufficiently to repeat its first record. If, instead of resting the completely fatigued muscle, further muscular effort is made, the period required by the muscle for recovering is greatly prolonged. This is in accordance with practical experience. The ergograph emphasises the ill-effects of straining the tired machine. The effect of hunger, want of rest, or mental activity, is found to diminish the amount of work produced. When the circulation in the muscle is improved by massage, more work is produced. The effect of improving its nutrition by food, especially by a readily soluble and easily absorbed substance such as sugar, is said to be to increase quickly its power of performing work. Finally, the effect of making a prolonged call for work upon one group of muscles is to diminish the activity of the others. The results obtained by the ergograph are those which accord with experience, but it is unfortunate that the personal element cannot be excluded from the experiments, especially where the questions of food and work are concerned.

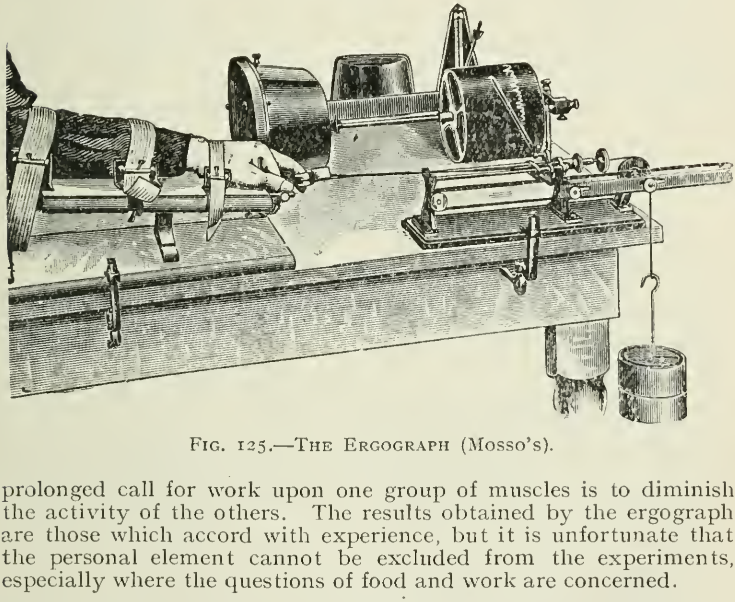

Fig. 125.—The Ergograph (Mosso's).

In connection with the work done by muscle, it is interesting to institute a comparison between the work yielded by the animal body and that by a well-constructed machine. The best triple-expansion engine may yield as work some 10 to 15 per cent. of the available energy in the fuel, the balance being lost as heat.

A muscle is more nearly allied to an internal combustion engine, and the efficiency of this is greater than that of a steam-engine. A large gas-engine may have an indicated efficiency of 34 per cent., which is 90 per cent. of the maximum possible. The small engine of a motor-car is relatively better, for under favourable conditions 28 per cent. of the potential energy in the petrol may be given off as work.

Experiments made on the horse by Zuntz show that 33 per cent. of the body substance katabolised during labour is recovered as effective work. This is described by Armsby as net efficiency, as certain deductions have been made; for instance, it does not include the effort required to move the animal's own body weight. It is obvious, however, that the net efficiency will be affected by the weight of the load drawn or carried, by the pace, also by whether the work is performed on a level or on an incline, and by the degree of gradient. So difficult are these questions to settle by experimental inquiry that 33 per cent. under favourable conditions must be interpreted broadly; with a gradient of 1 in 12 the efficiency was reduced to 23 per cent. Nevertheless, we are shown that the work performed by muscles is not inferior to that of the best internal combustion engine.

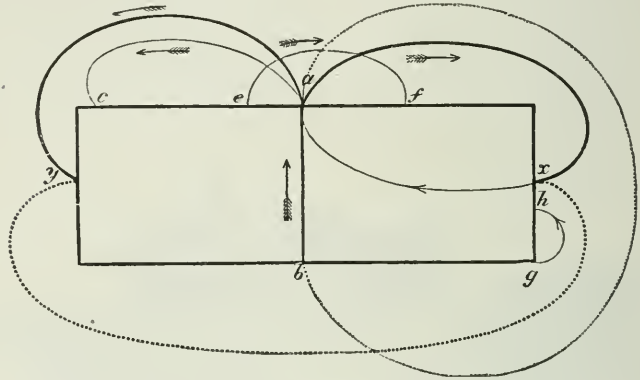

Fig. 126.—Diagram illustrating the So-called Electric Currents of Rest (Injury Currents) of Muscle and Nerve (Foster).

Being purely diagrammatic, the figure may serve either for a piece of muscle or nerve, excepting that the currents at the transverse section cannot be shown in a nerve. The arrows show the direction of the current through the galvanometer.

a, *b*, The equator. The strongest currents are those shown by the dark lines, as from *a* at the equator to *x* or to *y* at the cut ends. The current from *a* to *c* is weaker than from *a* to *y*, though both, as shown by the arrows, take the same direction. A current is shown from *e*, which is near the equator, to *f*, which is farther from the equator. The current (in muscle) from a point in the circumference to a point nearer the centre of the transverse section is shown at *g*, *h*. From *a* to *b*, or from *x* to *y*, as indicated by the dotted lines, there is no current.

Other interesting points were ascertained by Zuntz's work. He found, for instance, that work on a slight ascent was performed more economically than work on a dead level, and this is supported by practical experience. In the days of mail-coaches the horses did not last as long on a level road as on one where there were slight gradients, the explanation being that the slight rise and fall brought different groups of muscles into play, and so afforded a rest to others. Another curious fact brought out by Zuntz was that, though the ox climbed an incline with much the same efficiency as the horse, on a level he expended more in the transport of his own body weight than the horse. These questions will again come under notice in the chapter on Locomotion.

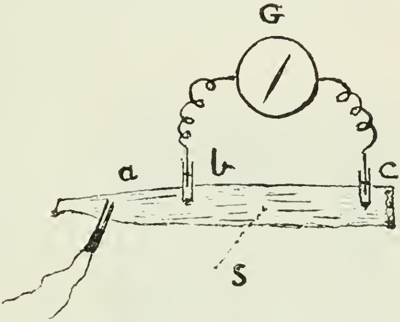

Fig. 127.—Sartorius Muscle arranged to demonstrate the Diphasic Variation of Action Current in Muscle (or Nerve).

S, Sartorius; *a*, stimulating electrodes; *b*, *c*, non-polarisable electrodes as 'leads' to *G*, the galvanometer. The electrode *c* is intentionally not placed on the injured end of the muscle, as it would be for demonstrating 'negative variation,' since the strong negativity of the injured end would mask the desired phenomenon. A similar arrangement suffices to demonstrate the same phenomenon in a piece of nerve.

Muscle Currents. — Great controversy has taken place as to whether currents of electricity exist naturally in uninjured muscle. It is found, for instance, that a piece of muscle isolated from the body, and placed in connection with a galvanometer, may be made to demonstrate the presence of electric currents which behave in a perfectly regular manner in passing from one definite point on the muscle to another. These are the so-called natural *muscle currents*, or **currents of rest**; they are found to pass in a certain direction—namely, from the longitudinal surface of the muscle to the cut extremity. The natural surface of the muscle, therefore, corresponds to the copper of a Daniell's cell, the cut ends to the zinc element; the surface of the muscle is in consequence galvanometrically positive, the cut ends galvanometrically negative (see p. 428). The more the ends are injured the more galvanometrically negative they become. It is now known that the *currents of rest* in muscle are caused by the *injury* inflicted on the muscle in its course of preparation for the experiment. They are in consequence frequently described as **injury currents.** Muscle at rest and absolutely uninjured gives *no current whatever*.

If while the galvanometer is registering the direction of an injury current the muscle preparation be stimulated with an interrupted current, a backward swing of the needle of the instrument towards zero indicates that the injury current is diminished; this diminution is termed the **negative variation.**

If an *uninjured* muscle, which is giving no currents, be stimulated by means of an interrupted current into contracting activity, it exhibits electrical phenomena, called the **current of action.** It is the production of this current which accounts for the negative variation of the injury current. The action current is of such a nature as to give rise to what is known as a *diphasic* variation in the current of a muscle, as shown by the needle of the recording galvanometer swinging first in one and then in the opposite direction. The double variation is due to the fact that the point on the muscle to which the stimulus is applied becomes negative to all points of the muscle at which the wave of contraction resulting from the stimulation has not yet arrived. This negativity occurs during the 'latent period' (p. 429), and passes along the muscles as a wave which precedes, or in some cases accompanies, the wave of contraction. Thus if, as in Fig. 127, a muscle be stimulated at *a*, while the points *b* and *c* are connected through a very sensitive galvanometer, at the moment of stimulation *a* becomes negative to the rest of the muscle. As this negativity sweeps along the muscle it passes first over the point *b*, which thus becomes negative to *c*, and the current in consequence flows from *c* to *b* through the galvanometer. Midway between *b* and *c* is a neutral point, as shown by the fact that when the electrical excitation reaches this point, no current is passing through the galvanometer. Immediately afterwards the current passes over the point *c*, and *c* then becomes negative to *b*, as shown by the current flowing through the galvanometer in the opposite direction. Every contraction of a muscle gives rise to a diphasic variation, which passes along the muscle slightly in advance of the contraction wave. These phenomena, while of the greatest interest in the case of muscle, become still more important in the case of a nerve, since they provide the only accurate means of following the passage of an impulse along a piece of *isolated* nerve, which does not, as does a muscle, change its shape or exhibit other obvious changes when stimulated.

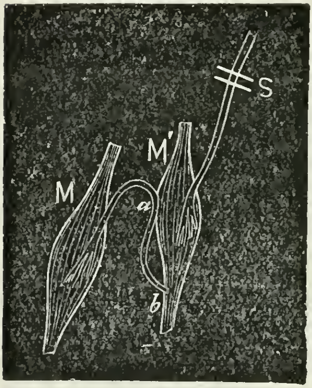

FIG. 128.—SECONDARY CONTRACTION.

The electrical change in muscle can be observed without the assistance of any apparatus by means of an experiment as old as electricity itself. As employed by Galvani, it was described as electricity without metals. The nerve of a nerve-muscle preparation (M, Fig. 128) is brought into contact with another muscle, M′, in such a way as to touch at two points—*e.g.*, the cut end *b* and the surface of the muscle *a*. The current of injury in the latter travels along the nerve, and produces a contraction in M. With the same preparation it can also be shown that if M′ be stimulated at S and made to contract, the negative variation which accompanies the contraction of M′ will produce a contraction of M. This is known as a 'secondary contraction,' while the above preparation is spoken of as the *rheoscopic frog*.

The electrical phenomena in muscle are not isolated examples of electric currents in the body. Closely similar phenomena are demonstrable in nerves, which we shall shortly study, and electrical changes accompanying their functional activity occur in secreting glands, in the eye, and to the highest degree in the electrical organs of certain fish. These electrical organs are modified muscle or skin glands.

Chemical Changes in Active and Resting Muscles.—The physiological changes occurring in muscles are remarkably active. The processes which result in muscular contractions use up at every moment the combustible material contained within the muscle structure, and the products arising from metabolism have to be got rid of at once and repair brought about. Changes are also constantly occurring even during the period of muscle rest. Muscle activity is characterised by muscle waste, muscle rest is characterised by a preponderance of the process of repair; we must therefore learn the nature of the waste and repair occurring in muscles.

The oxygen carried to resting muscles by the blood is absorbed in considerable quantities, and a volume of carbon dioxide, in slightly less quantity than corresponds to the oxygen absorbed, is returned to the venous blood. Whether a muscle is at rest or active, it is always absorbing and storing up oxygen, and giving off carbon dioxide. From this we might imagine that muscle would readily yield free oxygen, but as a matter of fact none can be obtained from it, and as carbon dioxide cannot be formed without oxygen, it is assumed that the muscle molecules store up oxygen in some form. That such storage occurs appears undoubted, for a nerve-muscle preparation can continue to contract when placed in a jar of nitrogen, and, what is even more remarkable, continues to produce carbon dioxide.

The storage of oxygen by resting muscle may, in the case of the cold-blooded frog, enable an excised muscle to yield some hundred contractions when suitably treated. In mammalian muscle, on the other hand, this quiescent store of oxygen does not suffice to maintain irritability for more than the briefest interval after the blood-supply is cut off. This is due to the much greater metabolic activity of mammalian muscle as compared with the muscle of the frog.

The amount of oxygen absorbed and carbon dioxide given off has already been considered (pp. 143, 145); the amount is greatly increased during work.

In the active muscle the bloodvessels are more dilated than in the muscle at rest, and this dilatation provides for the increased quantity of oxygen now required by the part. In experimenting on the lip muscle of the horse, Chauveau found that there was a fivefold increase of blood passing through the muscle during contraction as compared with rest. By means of the blood the irritability of the muscle—*i.e.*, its power of contraction—is maintained; whatever leads to a smaller quantity of blood being delivered to an active muscle produces partial or complete paralysis of the group or groups of muscles affected. This is well seen in a horse suffering from thrombosis of the iliac arteries; the blood-supply is sufficient during the time the animal is at rest, or even at a walk, but if he is called upon to trot, muscular cramps occur, followed by paralysis.

The study of metabolism has prepared us for the statement that the chemical changes occurring during contraction do not normally affect the nitrogenous elements of the muscle. The excretion of any increased amount of urea is variable, irregular, may not even take place, and is in no case remotely proportional to the work done. This is true as long as the body is supplied with a sufficiency of carbohydrates and fats. If these are deficient, then increased muscular activity does lead to an increased formation of urea, since the muscle now has to metabolise its proteins to provide the energy necessary for the work performed. Carbohydrates and fats are normally the chief sources of muscular contraction. The carbohydrates are represented by glycogen (formed, as we have seen, by the sugar brought to the muscle) and by dextrose. A well-nourished muscle contains 0·5 to 0·9 per cent. of its weight as glycogen. This local store of animal starch is, under the influence of an enzyme, converted back to sugar, and in this form is capable of yielding energy under the influence of oxidising enzymes. We have previously seen that the contraction of muscle leads to the disappearance of glycogen. In this condition, though free from glycogen, the muscle still continues to contract, there being sufficient sugar for the purpose existing in the blood, which even under starvation continues to maintain its normal 0·1 per cent. Under starvation this sugar is furnished by the breaking down of body protein, but under the ordinary condition of nutrition, when work has emptied the muscles of glycogen, there is ample sugar available from the store of carbohydrate taken into the body. Many circumstances seem to point to sugar as being preferable for the work of contraction. This is probably owing to the ease with which it can be oxidised, but it is quite certain that fat, which is more difficult of oxidation, may also furnish the necessary material used up in muscular work.

The formation of acid in muscle as the result of contraction has given rise to a good deal of inquiry. Lactic acid is found in muscle; it is not, as we have seen, the ordinary lactic acid found in milk, but a form optically active to which the name ‘ sarcolactic acid ’ has been given. Resting muscle contains only a trace of lactic acid (0·03 per cent.), while under the influence of contraction a marked amount is present (0·22 per cent.), and rigor, whether produced artificially by heating the muscle or naturally after death, leads to the production of as much as 0·3 to 0·5 per cent. The source of the acid is from glucose.

During muscular activity heat is produced; the blood returning from a muscle has a higher temperature than that going to it. Colin found the temperature of the masseter muscle of the horse to rise 5° F. through feeding. The whole body temperature is raised during work, especially in the horse, and does not fall for some time after. Haldane's observations show that the effect of a rise in body temperature during work is to heighten the excitability of the respiratory centre.

The Cause of a Muscular Contraction.—This is one of the most difficult problems in physiology, and has not been solved. There are many views, the most modern* being that potential energy is stored in the muscle in some unstable chemical form; by its decomposition lactic acid is produced, and the hydrogen-ions thus set free cause a change in the surface tension where the sarcoplasm and fibrillæ of the muscle are in contact; this leads to a condition of tension within the muscle, which consequently shortens and performs work. After contraction has occurred the lactic acid is oxidised, and the energy thus furnished is stored up for the next contraction. The production of lactic acid from glucose is more oxidative in character, but its removal after contraction has occurred needs an abundant supply of oxygen. During severe muscle exertion the whole of the lactic acid may not be so destroyed, in which case it is eliminated by the kidneys.

Fatigue.—The influence of fatigue on muscular contraction has previously been referred to. The cause of fatigue is the accumulation in the muscle of the chemical products of contraction. The material in muscles which gives rise to fatigue is sarcolactic acid, and by passing a solution of this acid into muscles the typical phenomena of muscle fatigue may be artificially induced. Similarly, as the blood of a fatigued animal contains fatigue products, transfusion of it into the circulation of a normal animal produces all the symptoms of fatigue. On the contrary, if a fatigued muscle be washed out with normal saline solution and a little weak alkali circulated through its bloodvessels, it becomes restored and regains its power of contraction. A muscle at work in the body is protected from ready fatigue by the ever-circulating blood, which supplies it with food and carries off the waste products of its activity.

Attention has been drawn to the fact (p. 423) that muscles are connected by elaborated nerve-endings with sensory nerves, to whose existence 'muscular sense' is due. The sensation of general fatigue which arises from excessive muscular exertion is due to a cerebral appreciation of the changes brought about in the muscles as the result of their contracting activity, and may be looked upon as a protective mechanism against straining the machine. Muscular activity implies the action of central nerve-cells, *neurones,* in which the impulses which give rise to the contractions of the muscles originate, followed by the passage of these impulses along the motor nerves, and their communication to the contractile fibres by the agency of the end-plates. Hence the phenomena of fatigue may be due to fatigue of the neurones, or of the conducting nerve fibre, or of the end-plate in the muscle, brought about by the injurious action of fatigue products. It is known that neurones and nerve fibres are practically impossible of fatigue, and accordingly the end-plate in the muscle itself has been looked upon as the seat of the failure. It is now, however, held that the junction of the motor-nerve with the neurone, the *synapse,* is the seat of fatigue. The energy in the muscle, excepting the organ be absolutely exhausted, is not entirely used up, for a fatigued muscle will contract on direct stimulation, when it is unable to respond to a normal stimulus conveyed through its nerve.

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* A. V. Hill, Fletcher, Hopkins (see 'The Physiology of Muscular Exercise,' by F. A. Bainbridge, M.D., F.R.S., 1919); also Professor Bayliss (see his 'Introduction to General Physiology,' 1919).

In the horse (the only animal subjected to fatigue, which is the cause of most forms of lameness from which it suffers) it is not on the muscles that the ill-effects fall, but on their tendinous attachments and the ligaments of the joints. This question is of extraordinary practical importance, and in dealing with locomotion the matter will be treated more fully; but the point which it is desired to emphasise here is that when muscles tire the strain of locomotion falls on tendons and ligaments, and these may, in consequence, rupture, as a rule incompletely, but sometimes completely. Rupture of muscle, however, is not unknown; the flexor of the metatarsus is a classical example, but rupture of a muscle is as a rule associated with violent muscular contraction such as a fatigued muscle is incapable of exercising. So powerful may a muscular contraction be that, should the muscle withstand the strain, bones directly or indirectly under its influence may be fractured. Most cases of broken back occurring when a horse is cast for operation are due, not to the concussion of the fall, but to the subsequent struggles; under these conditions the neck of the ilium may even be fractured.

A rupture of the diaphragm (see p. 157) is not due to muscular contraction, but to intra-abdominal pressure, especially tympanites, and in such cases it is the tendinous and not the muscular structure which gives way.

‘ Condition.’—That remarkable state of the body described as condition,’ into which horses can be brought by care in feeding, general management, and carefully regulated work, must be regarded as the state of highest perfection which muscles can attain. In its *highest* degree it is not a permanent state; no horse can remain in it for any length of time, and many can never be got into condition for severe work. It is easy in the training of horses to overstep the mark and produce ‘ staleness,’ a result which, like the fatigued muscle on the myograph, is usually recovered from by a short judicious rest, to which the system immediately responds.

During training all superfluous fat and water are removed from the body, the muscle-substance is built up, necessitating an abundant supply of protein, and the respiratory capacity increased. It is very necessary to remember that condition, though judged of largely by the state of the muscles, implies the proper working of the respiratory and circulatory systems. In order to sustain severe and prolonged muscular exertion an adequate supply of oxygenated blood must be sent to the muscles; this necessitates a rapid flow of blood and adequate ventilation in the lungs, with strong regular pumping power in the heart; all these factors must work in harmony. As a matter of fact, the ability to endure the strain of violent muscular efforts is far more dependent on the respiratory and cardiac mechanisms having been trained than on the skeletal muscles. Long walking exercise is given as a muscle developer, and judicious gallops to give an animal its ‘ wind,’ yet as a matter of fact the ‘ wind ’ is largely a question of heart. The heart must be large and muscular.* In the horse there are 29 litres (51·04 pints) of blood flowing through it every minute during rest; during work its output is doubled, or even quadrupled, depending upon the pace. Under stress it fills the pericardial sac. The filling of the heart is a question of venous inflow; if more is being returned than the ventricle can get rid of, it accumulates in the auricle, and when horses are galloped to death it is the auricle which ruptures, generally the right, owing to the resistance offered by the congested condition of the lungs. The amount of blood returned to the heart at both auricles must, broadly speaking, be the amount leaving it by both ventricles. A deficiency in this mechanism leads to ‘ loss of breath ’; clogging in the lungs means deficient oxygenation in the tissues, and without an adequate supply of oxygen the muscles are powerless to contract. We are clearly shown, from what may be witnessed in the hunting-field, or wherever horses are exposed to long-continued strain, that the chief value of training lies in the functional improvement of the muscular tissue of the heart and of the circulatory system in the lungs; both of these have to be educated to withstand the extra strain imposed. The only bloodvessels which commonly give way are the pulmonary. A rupture of the aorta is very rare.

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* For all we know, the difference between a failure and a success on the turf may be a few ounces more or less of heart muscle. A few additional ounces may represent a fortune !

The respiratory movements, as we have learnt, are dependent upon the rhythmic activity of the respiratory centre (p. 137). The powerfully stimulating influence on the respiratory centre of the waste products of metabolism resulting from muscular contraction has suggested to some that 'wind' may be the result of an increased immunity of the centre to the action of these products.

The voluntary muscles have also to be educated to work in the best and most economical manner; they must be used to advantage, smoothly and in combination; their response must increase in rapidity and power; they must grow and become hard. Sherrington* points out that in properly balanced muscular movements there is between each successive contraction a period of rest which is recuperative in nature and opposed to fatigue. One feature in training, which will be more fully appreciated when the study of the nervous system has been made, is the self-education of muscles in the importance of momentary rest following contraction, while the peculiar innervation of muscles, known as 'reciprocal,' is also improved by education, which insures that antagonistic muscles offer little or no resistance to their opponents.

Unpractised movements are a serious source of wasted muscular effort; by practice the same work can be performed with a greatly reduced expenditure of energy. In man it has been shown that the abnormal use of certain muscles, such as a soldier with an ill-fitting boot would employ when marching, produces extravagant combustion and early fatigue. This applies with equal force to the horse; ungreased axles, badly-fitting harness and saddles, sore backs and lameness, all mean excessive wear and tear. Zuntz found that a lame horse at work expended 99 per cent. more energy than one which was sound, also that a 'high stepper' required 33 per cent. more oxygen for doing the same amount of work as a horse without exaggerated action. Condition may further be defined as fitness for the particular class of work required; if horses are used for saddle work without being conditioned to carry weight, they fail; an animal may be in perfect condition for draught work, but quite unfit to carry weight, as the muscles are uneducated. In other words, there is a special education of the muscles for the particular class of work required, and until horses are 'conditioned' they cost more and do less work than the trained article. The only way in which this education can be effected is by training. The art of the trainer lies in employing a suitable resistance gradually and skilfully increased, and it requires long practice and experience. The physiologist can assist, as the pulse, respirations, temperature, and body excretions are an unfailing guide to the progress made.

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* 'The Rôle of Reflex Inhibition,' *Science Progress*, No. 20, April, 1911.

In the following table is shown the mean of forty-five observations on fit and a similar number of unfit horses performing identical work and carrying the same weight:

Average Pulse Rate before Work.	Average Respiration Rate before Work.	Pulse Rate at End of Work. (Taken for 15 Seconds.)			Respiration Rate at End of Work. (Taken for 15 Seconds.)		
		At Cessation.	Two Minutes after Stopping.	Five Minutes after Stopping.	At Cessation.	Two Minutes after Stopping.	Five Minutes after Stopping
Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.	Per Minute.
Fit Horses.							
40	10	88	55	46	41	21	16
Unfit Horses.							
39	12	113	66	56	48	28	19

The table shows that the pulse and respirations of fit horses are less disturbed by work, and more rapidly subside to normal after work, than those of unfit. In the above series the heart and respiration rate of the 'fit' subsided in two minutes to a point only reached by the 'unfit' in five minutes.

Chemical Composition of Muscle.—A dead muscle does not possess the same chemical composition as one which is living, and living muscle cannot be analysed without killing it by the methods necessarily employed. Thus any tabular statement of the quantitative composition of muscle gives really the composition of dead muscle. We are, however, assisted to some knowledge of the nature of living muscle-substance by the following facts:

If contractile, and therefore living, frog's muscle is carefully frozen and then very slowly thawed, it does not lose its irritability: it is still alive. When frozen, it may be minced with a cold knife and ground up in a cold mortar with four times its weight of snow containing 1 per cent. of sodium chloride. By this process a viscid liquid is obtained which may be filtered, though with difficulty, at 0° C. The fluid filtrate is opalescent, neutral, or faintly alkaline in reaction, and is known as 'muscle-plasma.' When its temperature is allowed to rise it coagulates in the same way as does blood-plasma, yielding a *clot* which, unlike fibrin, is granular and flocculent, and forming a liquid *serum*. During the clotting the liquid becomes acid, as the result of a formation of *sarcolactic acid*, and the clot consists of *myosin*. Assuming, as we may reasonably do, that the muscle-plasma represents more or less closely the muscle-substance in the living fibre, we may take these phenomena of the clotting of the muscle-plasma as indicating the most characteristic chemical differences between living and dead muscle (though there are others), and thus we gain considerable insight into the composition of living muscle as based upon an analysis of the dead tissue.

With this preliminary caution we may now state the composition of muscle to be approximately as follows:

Water - - -	75 per cent.
Proteins - - -	20 ,,
Fat - - - -	3 ,,
Carbohydrates - -	0·4 to 1 per cent.
Nitrogenous waste products -	0·2 ,,
Salts - - - -	1 to 1·5 ,,

The nature of the proteins of muscle is a matter of uncertainty. It must suffice to say that the chief and characteristic protein of dead muscle is the *myosin* formed in the clotting of muscle-plasma; it belongs typically to that class of proteins known as *globulins*. Bearing in mind the phenomena of the clotting of muscle-plasma, and using the nomenclature employed for blood-plasma, we may say that living muscle contains *myosinogen*, which on the death of the muscle is converted into myosin, just as in blood-plasma fibrinogen gives rise to fibrin. It has not as yet been shown that calcium salts play a part in the coagulative formation of myosin, as they necessarily do in the production of fibrin and of the casein-clot in milk. All the proteins of living muscle are not entirely myosinogen, nor are all those of dead muscle myosin. Other members of the globulin class are present in both, as also an ordinary albumin closely resembling serum albumin.

The carbohydrate material is composed chiefly of glycogen, which diminishes in amount by conversion into sugar on the death or after the contracting activity of muscles; these substances have already been fully dealt with in a previous chapter. The nitrogenous waste products or 'extractives' are creatine, hypoxanthine (obtainable in the free form in muscle extracts), xanthine, carnine, taurine (in horse-muscle), uric acid in minute traces (more abundant in reptilian muscle), and probably traces of urea, though this is a question not yet decisively settled.

Of these, creatine is by far the most important; it is a substance which has already been studied in connection with the production of urea (p. 338). The ash in muscle consists principally of the salts of potassium and magnesium. The gases are carbon dioxide, together with a small amount of nitrogen, but no free oxygen.

In plain muscle glycogen is found only in traces, if at all; lactic acid and creatine are found in smaller quantities than in striped muscle. Hypoxanthine is conspicuously present, while, in contrast to striped muscle, the chief salts are those of sodium and calcium.

Rigor Mortis.—After death a muscle passes into the condition of rigor or stiffening, by which it changes both in its physical and chemical aspects. The muscle becomes firm and solid, loses its elasticity, and no longer responds to electrical stimuli; further, it loses its alkaline reaction, and in course of time becomes acid owing to the formation of sarcolactic acid. Through the death of the muscle its proteins pass from a fluid or viscous condition into a solid, and this process is generally believed to be identical with the clotting of muscle-plasma previously described. Rigor mortis and the production of sarcolactic acid are closely connected, so that if the formation of the acid be prevented by suitable means, rigor does not occur. The view now adopted as to the cause of death-stiffening is that it is due to a coagulation of the proteins by the products of metabolism in the muscle, and this explanation accounts for the rapid setting in of rigor in animals hunted to death. Rigor mortis is delayed in a rabbit in which the labyrinth of the internal ear has been destroyed; this is probably due to the fact that the labyrinth is somehow connected with the obscure problem of muscle tonus. The muscles in which delayed rigor mortis occurs are those of the same side of the body as the injured labyrinth. During rigor mortis carbon dioxide is produced and heat evolved; some after-death temperatures are remarkably high (p. 421). After a certain length of time rigor mortis passes off and decomposition commences. The remarks in Chapter XIX. descriptive of the attitude the body assumes after death should be read.

There is a condition of muscle known as **heat rigor**, which is produced by rapidly raising the temperature of a mammalian muscle to 47° C. (117° F.). It is very closely allied to death rigor, and is due to the same cause—*i.e.*, coagulation of the proteins. It differs from death rigor inasmuch as it does not pass away.

It is doubtful whether rigor mortis occurs in involuntary muscle; the post-mortem appearance presented in this variety of muscle may be due to cold, for it has been shown that two or three days after death smooth muscle may be warmed up so as to be capable of contraction.

CHAPTER XIV

THE NERVOUS SYSTEM*

SECTION I.

Classification of Nerves.—The first step towards a classification of nerves was taken when the discovery was made that some nerves are exclusively sensory and others exclusively motor in function; prior to this it was believed that a nerve could carry either impulse indifferently. It was next found that a nerve in the body could carry impulses only in one direction; for instance, a sensory nerve could only convey impulses from the periphery of the body towards a centre, a motor nerve could only convey impulses from a centre to the periphery. This is the real basis of classification, notwithstanding the fact that the impulses travelling to a centre, though spoken of as sensory, and those from a centre to the periphery, though motor, may be widely different in nature. The terms 'sensory' and 'motor' prove very misleading in speaking of the function of a nerve, and for long it has been recognised that the two great divisions of nerve fibres are **afferent,** or centripetal, and **efferent,** or centrifugal. An afferent nerve is one conveying impulses from the periphery to the centre, no matter what the nature of these impulses may be. An efferent nerve is one conveying impulses from a centre to the periphery, notwithstanding that these impulses may be of widely different characters. The determining factor of whether a nerve is afferent or efferent does not lie in its structure; the microscope reveals no difference between the two. The character of the nerve is determined by its physiological action and the nature of the nerve-ending in the tissues, and this is proved by the fact that one kind of efferent nerve may be made experimentally to take the place of another.

Afferent nerves, as we have seen, are those engaged in conveying impulses towards a centre; the centres are the brain, spinal cord, and masses of nerve tissue connected therewith, known as 'ganglia.' Whether the afferent nerves be those of special sense—*i.e.*, visual, olfactory, gustatory, and auditory—or those of touch, pressure, heat, cold, and pain, the widely different results obtained on stimulation depend upon the end-organ of the nerve, and not on any difference in the character of the impulses. There are afferent impulses constantly occurring which are not within the knowledge of the animal; they may be of an excitatory nature, or of a controlling or inhibitory character. We have studied this group characteristically in our consideration of the vascular and respiratory systems, pressor or depressor effects occurring in the circulation in consequence of excitatory or inhibitory impulses conveyed by afferent nerves, though not necessarily by the same afferent nerve. The same occurs also in the respiratory system. Nor are we limited for illustration to the two systems mentioned; we have met with it in muscle tonus, visceral movements, glandular secretion, and other phenomena.

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* I am indebted to Professor Sherrington, F.R.S., for kindly supplying that portion of this chapter which deals with the 'scratch,' and 'step' reflex.

Efferent nerves are those in which the impulses are passing from the centre to the periphery, and the largest system of efferent nerves in the body is that passing to the muscles. The term is used in its widest sense, for not only are the skeletal muscles supplied, but also, as we have already seen, the unstriped muscle of the viscera, bloodvessels, and body hairs, and the striped muscle of the heart. Nor are efferent impulses solely motor; they may be secretory; this we have studied in connection with saliva and gastric juice. Finally, the impulses may be inhibitory; they then control or prevent muscular movement, and control or prevent secretion.

It must not be supposed that all the tissues of the body are completely endowed with the nerve fibres described. Fibres for the bloodvessels, excitatory and inhibitory, are not found in all bloodvessels, and though excitatory efferent (motor) fibres exist largely in skeletal muscle, there are no inhibitory fibres to this tissue, a remarkable fact, which will be fully considered later, in view of its extraordinary physiological importance.

From the above it will be seen that a classification of nerves is not a simple matter, and physiologists are not agreed as to the best system to adopt. The afferent scheme given on p. 454 has been suggested by Professor Sherrington.

Personally we would add to the classification *trophic* nerves, or those engaged in nutrition. Some physiologists hold that special nerves governing nutrition do not exist, and that the process runs concurrently in the nerves governing wear and repair; the evidence that exists in favour of our belief will be mentioned in due course.

AFFERENT NERVES.*

Peripheral Distribution.			Sensation.			Stimulus.		Reflex Effect.
	General.	Local.						
I. From *surface* of organism	External (or cutaneous) surface, including mouth (*exteroceptive*)	Skin		Pain	Stimuli are all environmental	Any stimulus, chemical, thermal, mechanical, or electrical, so long as injurious (*nociceptive*)	Sensory and reflex effects both ample—*i.e.*, cerebral and post-cerebral reactions both intense	Postures and movements by skeletal muscles; circulatory and respiratory muscles.
				Warmth Cold		Temperature	.. ..	Circulatory, respiratory, and pilomotor muscles; sweat glands.
				Touch		Mechanical	Sensory effect more marked than reflex—*i.e.*, cerebral reactions > post-cerebral	Skeletal muscles.
		Cochlea	Distance sensations	Auditory		Mechanical (sound)		Muscles of ear, neck, and eyes.
		Retina		Visual		Radiation (light)		Muscles of eyes and neck.
		Nose		Olfactory		Chemical vapours and solutes	.. ..	Respiratory muscles; salivary and gastric glands.
		Tongue and palate		Taste		Chemical solutes	Sensory and reflex effects both marked: cerebral = post-cerebral	Muscles of mastication and deglutition; salivary and gastric glands.
	Internal (or digestive, urinary, and respiratory) surface (*interoceptive*)	Alimentary canal (fauces to anus)		None (? repletion and emptiness): abnormally pain	Stimuli are contents—*e.g.*, food, etc.	Mechanical and chemical	Sensory effect much less than reflex: cerebral reaction < post-cerebral	Visceral movements and secretions; circulatory changes, local and general.
		Respiratory tract		None: abnormally pain		Mechanical and chemical	Ditto	Respiratory muscles.
II. From *depth* of organism (*proprioceptive*)		Labyrinth (ear)		Sensations of positions and motions of head (abnormally vertigo)	timulation always, some part of the body itself acting as stimulus to the body's own receptors—*i.e.*, *proprioceptors*	Mechanical	.. ..	Postures (muscle-tone) and movements of eyes, head, and neck, and, to less extent, of limbs and trunk.
		Skeletal muscles (including tendons) joints and fasciæ.		Sensation of positions and motions of body and limbs—*i.e.*, muscular sense: abnormally cramps		Mechanical, chiefly stress or strain	Sensory effect less marked than reflex—*i.e.*, cerebral reaction < post-cerebral	Postures (muscle-tone) and movements of neck, trunk, and limbs: tendon reflexes, knee-jerk, etc.
		Visceral and circulatory muscles		None: abnormally cramps		Mechanical, chiefly distension	.. ..	Alterations of tone and rhythmic contraction of the visceral or circulatory muscles involved;

EFFERENT NERVES.

- Efferent nerves
  - Pressor
    - Motor
      - Motor to skeletal muscle.
      - Vasomotor.
      - Cardio-motor (not a true motor).
      - Viscero-motor, and includes respiratory(trachea and bronchi) and coat of spleen.
      - Pilo-motor and unstriped muscle of skin generally.
      - Iris and ciliary muscle.
    - Secretory
      - Salivary.
      - Gastric.
      - Sudorific.
  - Depressor
    - Inhibito-motor
      - Only known for heart, some bloodvessels, some parts of digestive canal, iris, and retractor penis.

Conduction in Nerves.—In considering the direction of the impulses conveyed by nerves as a basis of classification, there are two fundamental principles on which something more should be said. It has been shown that the effect produced by a nerve does not depend upon its structure, but upon the nature of its termination in the tissue. Many years ago, before the truth of this doctrine had been conclusively established, the writer had endeavoured to cure a local paralysis by dividing the paralysed nerve and suturing the peripheral end to the central end of a sound motor nerve. He found that when two sound nerves were so dealt with, motor impulses from an entirely new source provided the tissue with motor function, and, moreover, furnished it at the right moment—namely, at the moment the muscle was required to contract, and not during the period when it should relax. Subsequently Langley showed by a similar experiment that the functions of the chorda tympani and sympathetic on the bloodvessels of the submaxillary gland could be reversed. If the peripheral end of the sympathetic were united to the central end of the chorda, the effect was constriction and not dilatation of the vessels. Similarly, if the peripheral end of the chorda were united to the central end of the sympathetic, the vessels dilated on stimulation of the sympathetic instead of contracting. The essential structure was proved to be the nerve termination in the tissue, and not the nerve which carried the impulse.

It is on these lines that the writer has endeavoured to cure laryngeal paralysis in horses. But though he has succeeded, as stated above, in getting a sound left recurrent sutured to a sound spinal acessory to function properly, he has not succeeded in obtaining these results with a paralysed left recurrent, not even when the operation has been performed early, presumably before the end plates had undergone complete degeneration.

The other fundamental principle in nerve conduction relates to the law that the living nerve transmits impulses only in one direction—viz., either to the centre or to the periphery. When a nerve is removed from the body there is no difficulty in transmitting an electrical impulse in either direction, but within the body the law is as stated. We shall see presently that the dorsal roots of the spinal cord are sensory or afferent, but Bayliss has shown that if these roots from the fifth lumbar to the first sacral be divided, and the *peripheral* end stimulated, vascular dilatation of the vessels of the hind-limbs occurs. The assumption is, therefore, that efferent fibres are passing out of the cord through the dorsal roots, and conveying motor impulses to the bloodvessels in a direction opposite to that in which the ordinary sensory impulses pass. Bayliss has termed these impulses *antidromic*, as indicating they are occurring in the opposite direction to the natural stream.

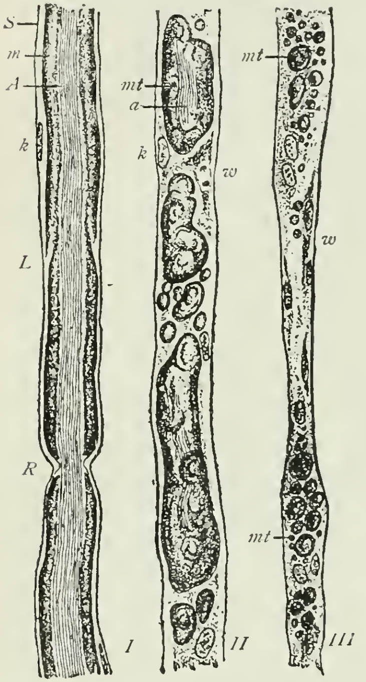

FIG. 129.—NORMAL AND DEGENERATED NERVE FIBRES (BARKER, AFTER THOMA).

I. Normal fibre: *S*, neurilemma; *m*, medullary sheath; *A*, axis cylinder; *k*, nucleus; *L*, Lantermann's line or cleft; *R*, node of Ranvier. II. Degenerating fibres: *mt*, drops of myelin; *a*, remains of axis cylinder. III. Further stage of degeneration: *mt*, drops of myelin; *w*, proliferating cells of neurilemma.

Structure of Nerves.—Nerves were originally grouped under two heads, according to their colour, as *white* and *grey*. The microscope revealed the fact that a difference in structure existed between them, the white fibres possessing a thick coating of fatty substance which gave them their colour, while the grey fibres were without this covering. The white substance is described as the medullary sheath; nerves so covered are termed *medullated*, while the 'grey fibres'—a term now rarely used—are spoken of as the *non-medullated*. If a **medullated nerve** be examined microscopically (Fig. 129, I), it is found to consist of a central core, or *axis cylinder*, consisting of fibrils, surrounded by a white substance known as the *medullary sheath*, and outside this is another sheath, or *neurilemma*. The medullary sheath does not extend continuously along the nerve; it is broken at intervals, termed *nodes*. The portion of nerve included between two nodes has a nucleus somewhere in it lying beneath the neurilemma. A bundle of such fibres enclosed in a sheath—and they may number thousands to the bundle—constitutes a nerve. A **non-medullated nerve** resembles the above in every respect, excepting in the medullary sheath. Of this it has none. It consists of an axis cylinder covered by a neurilemma. The fibre is freely nucleated, and a bundle of such fibres in a sheath constitutes a non-medullated nerve. This class of nerve belongs solely to one branch of the nervous system—viz., the sympathetic —whereas the medullated fibres are confined to the larger system of cerebro-spinal nerves.

The essential feature in the nerve is the axis cylinder; it is the true impulse-conducting substance. The function of the medullary sheath is not definitely known; it has been assumed to play the part of a non-conductor and insulate one fibre from another, but evidently this does not exhaust its uses, for, as just mentioned, the fibres of the sympathetic system are without a medullary sheath. Even medullated nerves lose their sheath before terminating in the tissues. Medullated nerves are more sensitive to stimuli than non-medullated, and the longer the nerve the greater the thickness of the sheath, but at present these facts cannot be connected with function.

The axis cylinder, as previously stated, is *the* important part of the nerve; it is the conducting substance, and its nature and origin are of the utmost significance. We shall see presently that the entire nervous system consists of nerve-cells and fibres. The nerve-cell is the essential feature, and no matter whether the brain, spinal cord, or ganglia be examined, nerve-cells characteristic of the tissue are present; the nerve-cells of the cerebellum are absolutely distinct from those of the cerebrum; the cells in the ganglia are different from either, or from those found in the spinal cord. It does not matter how greatly the nerve-cells differ in type, they all conform to one law, and that is they each furnish from one pole of the cell a process which becomes a nerve-fibre. No cell furnishes more than one such process, and that process constitutes the axis cylinder of the nerve. When the neurone doctrine is dealt with, more will be said on this subject, but one item of information must be anticipated, and that is a nerve-fibre is really an elongated process of a nerve-cell, and may run for a considerable distance without a break; even when it is broken the thread is again taken up, so that the axis cylinder runs from its origin to its termination. There is no union of nerve-fibres; of the thousands in a large bundle each and every one is complete in itself, and it is this which enables the same nerve-trunk to convey impulses of many and opposite kinds. Of such a nerve-trunk no better example could be given than that of the vagus, with its fibres to the larynx, lungs, heart, stomach, and intestines, each functioning in its own way and independently of its neighbours, with which it may have no more in common than if they did not exist.

Nerves are remarkable for their want of elasticity, but they are capable of very considerable stretching without breaking. In man the nerves of the limbs require a weight of from 18·2 kilogrammes (40 pounds) to 54·6 kilogrammes (120 pounds) to break them. Nerves are also very indifferently supplied with blood-vessels.

Nerve Terminations.—There are some structures, such as glands, where the nature of the nerve termination is not satisfactorily made out; there are other places, such as muscle, where definite and distinct motor nerve-endings have been found; and on many sensory and sympathetic nerves special terminations, known as 'Pacinian corpuscles' and 'Krause's end-bulbs,' exist. Nerve terminations are found in the muzzle of animals, in tendons, in muscles, in the generative organs, conjunctiva, mouth, tongue, epiglottis, etc.; some are known as 'Krause's end-bulbs,' those in tendon are described as the 'organ of Golgi,' in muscle they are known as 'end-plates,' whilst in the skin of the muzzle the nerves terminate in small swellings or enlargements known as 'tactile cells,' which are placed between the epithelial cells of the epidermis; cells of this kind also exist in the foot of the horse. The nerves of special sense have each a distinct termination peculiar to themselves, such as the hair-cells of the internal ear, the rods and cones of the retina, taste-bulbs of the tongue, etc.

Chemistry of Nerve-Fibres.—The chemistry of these tissues is very imperfectly known. Advances in physiological chemistry have shown that substances like *protagon*, which at one time was believed to represent the essential composition of the medullary substance or myelin, are really a mixture of substances. The myelin furnishes three substances which possess definite chemical characteristics—viz., cholesterin, lecithin, and cerebrosides. *Cholesterin* is a substance containing neither nitrogen nor phosphorus, and in chemical nature is allied to a group of bodies found in plants known as *terpenes*. Its silvery crystalline formation is characteristically shown in the tumours on the choroid plexus of the horse. In the body it occurs with lecithin, though the nature of the physiological connection, if any, is unknown. *Lecithin* is a phosphorus-containing nitrogenous fat, especially characteristic of the nervous system, but found elsewhere in the body. When lecithin is decomposed it yields, among other products, a fatty acid; it is this which is blackened in osmic acid staining of normal and degenerated fibres. *Cholin*, another product of the decomposition of lecithin, is very poisonous. *Cerebrosides* are a group of glucoside bodies containing nitrogen, of which very little is known, excepting that they yield galactose on decomposition.

Irritability and Conductivity.

Two features of nerve-fibres are irritability and conductivity. By irritability is understood the reaction to a stimulus, by conductivity the propagation of an excitation. The nature of the change occurring in a centre or receptive surface which induces an impulse is as yet unknown, but whatever the change may be it is experimentally possible to imitate it artificially by means of chemical, mechanical, or electrical stimuli, and when nerves are so stimulated they function as if the normal stimulus had been applied. Electrical stimuli are most commonly employed, and if a motor nerve be so stimulated the muscle contracts; if a sensory nerve, pain or a sensory impression is observed. If a secretory nerve be stimulated, secretion results. At one time the normal stimulus to a nerve-cell was believed to be electrical in nature; it is now known that this is not so, and that though electrical stimuli are capable of causing a nerve to function, this is a coarse method compared with the natural stimulus. A sudden change in temperature acts as a stimulus to a sensory, but not to a motor nerve. A motor nerve is quite unaffected by sudden cooling or heating, whereas a sensory nerve so treated produces pain, and it has been suggested that this difference in reaction indicates some marked difference in structure. When nerves are ligatured or divided impulses are no longer transmitted. Experimental inquiry shows that even after long-continued excitation nerves are still irritable, which has given rise to the belief that they never suffer from fatigue (see p. 446).

The stimulation of a nerve-muscle preparation by means of a weak constant current causes a ‘ twitch ’ of the muscle at ‘ make,’ and another at ‘ break ’; during the period the current is passing through the nerve, though the muscle gives no evidence of this, yet important changes are occurring. These changes are concerned with the irritability and conductivity of the nerve, and must here be examined.

Electric Phenomena in Nerves.—When studying a muscular contraction, we saw that a perfectly uninjured muscle was *iso-electric*—viz., it gave no evidence to the galvanometer of the existence of a current. If, however, the muscle was injured, the seat of injury became electrically negative to the uninjured part, and the current was called the **current of injury.** The figure there employed to explain injury currents in muscle is again used here to explain the same currents in nerves. If the nerve be injured, the current of injury flows from the equator to the cut end outside the nerve, and from the cut end to the equator inside the nerve. If a nerve, while exhibiting the presence of a current of injury, be stimulated, the uninjured portion becomes electrically negative to the injured part. There are now two currents in the nerve—viz., the current of injury and the new one just created; each is flowing in the opposite direction, the result being that the current of injury becomes diminished. This diminution or reduction in the current of injury is termed **negative variation.**

In the two observations described the nerve is assumed to be in an injured condition. If now a constant current be passed through

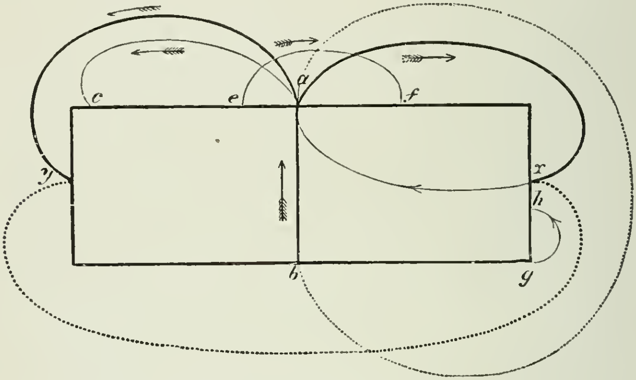

Fig. 130.—Diagram illustrating the Electric Currents of Injury in Nerve and Muscle (Foster).

The diagram serves either for nerve or muscle, excepting that the current *gh* is not present in nerve. The strong currents are shown by the dark lines; the arrows show the direction through the galvanometer. *ab*, The equator; *ax*, current from equator to cut end; *xa*, current within the nerve, cut end to equator.

an uninjured nerve, a wave of electrical negativity travels along it, and this current is termed the **current of action.** It will be obvious that it was the presence of the current of action which diminished the current of injury in the previous experiment. Let a nerve be taken and arranged as shown in Fig. 131, A—viz., a constant (polarising) current passed through its middle piece, while a galvanometer is connected with both regions of the nerve outside the anode and kathode poles of the battery. Under these circumstances, a polarising current passes through the nerve in the direction of its circuit—viz., from anode to kathode and back to the battery; but, in addition to this, there is a current in the extra-polar regions, as indicated by the attached galvanometers. These extra-polar currents are termed **electrotonic.** The piece of nerve beyond the kathode is increased in excitability and conductivity, and this is termed *kath-electrotonus.* The portion of nerve beyond the anode is decreased

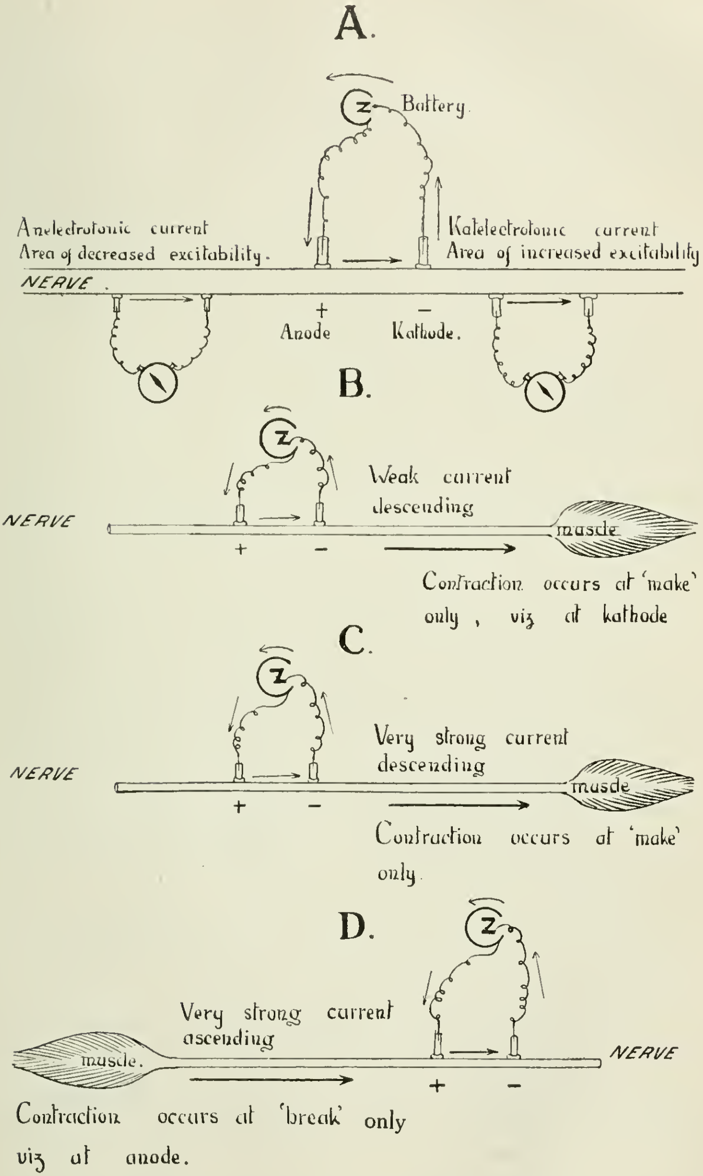
A.
Battery.
Anelectrotonic current
Area of decreased excitability.
Katelectrotonic current
Area of increased excitability
NERVE.
+
Anode
−
Kathode.
B.
Weak current descending
NERVE
muscle
+
−
Contraction occurs at 'make' only, viz at kathode
C.
Very strong current descending
NERVE
muscle
+
−
Contraction occurs at 'make' only.
D.
Very strong current ascending
muscle.
NERVE
+
−
Contraction occurs at 'break' only viz at anode.

FIG. 131.—DIAGRAM OF ELECTROTONUS.

in excitability and conductivity, and is in a condition known as *anelectrotonus*. It will be observed that, though the battery current is sent only through the middle piece of the nerve, it gives rise to a current which passes through the whole length of the nerve in the same direction as the exciting current, as shown by the galvanometers. Turning again to Fig. 131, A, it is evident that between the region of increased and that of reduced irritability there must be a region of neither increased nor diminished irritability. This is known as the *neutral point*. When the polarising current is weak, this point is nearer the anode; when it is strong, it is nearer the kathode, so that with very strong currents the whole intrapolar region may be in a condition of anelectrotonus. A clear understanding of this fact will render the subsequent observations intelligible. It will be remembered that the muscle of a nerve-muscle preparation gave, on stimulation, a twitch at 'make,' and another at 'break,' the make contraction always starting from the kathode, and the break contraction from the anode. These contractions are due to the development of electrotonic currents, and, provided the stimulating current always remains of the same strength, the twitch at 'make' and another at 'break' will always be obtained. But it is known that an increase or decrease in the strength of the polarising current gives other results in the muscular response; for instance, if the current be weak (Fig. 131, B), contraction of the muscle occurs only at 'make,' the kathode end of the nerve being the region of increased excitability and conductivity, the anode end being in both these respects decreased, and with a weak current lowered below the point of possible electrical response. If the current be made stronger, contraction occurs both at 'make' and 'break.' If a very strong descending current be passed through the nerve, contraction occurs at 'make' only, owing to the area of increased excitability lying next the muscle (see Fig. 131, C). If the muscle be attached to the opposite end of the nerve—viz., nearest the anode pole—and a very strong current sent through, the battery current will be passing up the nerve, as it is termed—*i.e.*, from the muscle to the spinal cord (Fig. 131, D); under these conditions there is no difficulty in a 'break' contraction occurring, as the area of increased excitability is again in the myopolar region; but the reduced excitability and conductivity of the nerve prevents the current from reaching the kathode, so that no contraction occurs at 'make.' Pflüger, who investigated these phenomena, formulated a **Law of Contraction**, which, after the above explanation, may now be stated:

Strength of Current.	Ascending Current.		Descending Current.	
	Making.	Breaking.	Making.	Breaking.
Weak -	Contraction	No contraction	Contraction	No contraction
Moderate	Contraction	Contraction	Contraction	Contraction
Strong -	No contraction	Contraction	Contraction	No contraction

When a particularly irritable nerve-muscle preparation is stimulated with a constant current, it may pass into tetanus at either 'make' or 'break.' This is known as *Ritter's tetanus*. The nature of electrotonic currents is not fully agreed upon; they are markedly shown in fresh medullated nerves, but not in those which are dead; they are only feebly shown in non-medullated nerves. Though physical in origin, they can be obtained only in nerves which still possess the characteristics of living. They may be demonstrated in an artificial nerve in which the axis cylinder is represented by platinum wires, and the medulla by a glass tube containing a solution of zinc sulphate. It is believed that electrotonic currents are due to polarisation occurring between the medullary sheath and axis cylinder, but nothing is yet settled.

The facts which have been ascertained experimentally as to effects which follow the application of constant and induced currents have been employed in the diagnosis of nerve degeneration. A healthy motor or sensory nerve, or healthy muscle, reacts to both stimuli. A degenerated nerve conveys no sensory impulses, nor is stimulation of a motor nerve so affected followed by muscular contraction. Muscles in the horse, if we except the effect of azoturia, do not appear to suffer from atrophy, unless as the result of injury or degeneration of the nerves. A muscle will grow smaller if thrown out of use, but the result is very different from the atrophy occurring in consequence of nerve degeneration, which is remarkable for its completeness and the relative rapidity with which it occurs. Muscle fibres will respond to direct stimulation of a constant current, even when the nerve is degenerated; but the contraction is slower, and is brought about, not through the nerves, but through the muscle fibres. A healthy muscle responds as readily to a constant as to an induced current. With complete degeneration of a motor nerve, no response on its stimulation is evoked from the muscle; nor can the latter be stimulated by induction shocks, but it may be stimulated by the constant current. This is employed in human practice as a test of degeneration. A normal contraction, we have seen, occurs at the negative pole on closing. To obtain a contraction at the positive pole on closing, a stronger current must be employed; but in paralysis, which is not of central origin, the muscles do not respond to an induced current, but react to a continuous current, and the same strength of current, both of opening and closing, will readily produce a response. This is the *Reaction of Degeneration*.

Negative Variation.—We have seen (p. 460) that when a nerve is indicating through the galvanometer the existence of a current of injury, its stimulation leads to a current in the opposite direction, or negative variation. In living nerves negative variation has been observed in consequence of stimulation of the brain, and the association of negative variation with normal nerve impulses is accepted. Negative variation marks in a nerve what a contraction represents in a muscle—viz., the passage of an impulse. The capillary electronometer shows that the onward rush of negativity travels at the same rate as a nerve impulse. By means of the string galvanometer of Einthoven (an instrument far surpassing the capillary electronometer in delicacy), a negative variation may be seen to occur in the vagus at each inspiration. Movements due to an electrical change can be detected passing both up and down the nerve in consequence of nervous impulses.

Diphasic Variation.—When a muscle contracts, a wave runs along it, and an electrical change occurs. The contracting part of the muscle becomes negative, and then, as the muscle returns to the state of rest, this negativity disappears. This two-phase electrical condition is termed *diphasic variation*; its presence in muscle is concurrent with a contraction, while in nerve it is identical in point of time and rate with the transmission of a nervous impulse. We have seen that the current of injury may be detected by the rheoscopic frog; the current of action may be detected in the same way. If the nerve of a nerve-muscle preparation be laid on the heart of a frog which is still active, the current of action liberated from the heart by its contraction causes the muscle of the limb to contract at each heart-beat.

The string galvanometer shows that when a muscle contracts two electrical waves pass over it, due to changes in potential. Electrometer records of the contraction of the heart muscle may be obtained by placing leads either on the exposed heart, or leading off through the limbs. Waller was the first to show how an electrocardiogram could be obtained in an intact animal at each beat of the heart. If a dog be placed with one fore-paw in a basin containing a solution of salt, and a diagonal hind-paw in another, and the two basins connected with the galvanometer, at every beat of the heart the electrical changes resulting from its contraction are conducted through the body to the electrometer, and the minute movements of the mercury rendered visible by a microscope. Contraction begins at the base of the heart; the base is therefore negative to the apex. When the ventricles contract, the cardiogram shows that the apex is then negative to the base; the interpretation of the curve is not, however, so simple as might appear.

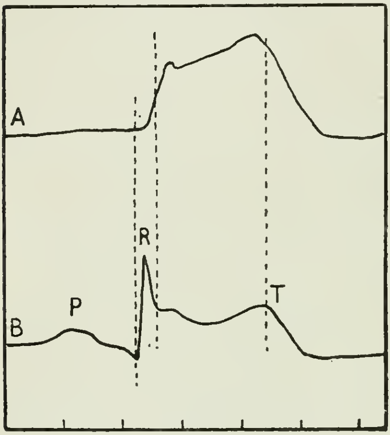

Fig. 132.

Simultaneous records of *A*, intraventricular pressure; *B*, electrocardiogram of cat's heart; *P*, corresponds to the auricular systole; *R* and *T*, to the ventricular systole (modified from Piper).

(From Bayliss' 'Principles of Physiology.')

The electrocardiogram represents the algebraic sum of the electrical changes taking place at the two electrodes (base and apex). As is evident from the figure, the electrical changes slightly precede the form or pressure changes.

Nature of Nerve Impulse.—The velocity of a motor impulse in man has been ascertained to be about 100 metres (333 feet) per second; the velocity in sensory fibres is unknown. In the frog the velocity of the action-current in motor nerves agrees exactly with the rate at which a motor impulse travels along the nerve, and in discussing the nature of nerve-impulses it is natural that the action current (negative variation) should be considered to be intimately connected with the transmission of ordinary normal impulses. It is necessary, however, to be careful and avoid considering this change and a nerve impulse as identical.

The most valuable additions to our knowledge of the subject of nervous conduction we owe to the work of Keith Lucas* and his school, which deals with the phenomena exhibited by conduction along peripheral nerve-fibres. The problems which have received most careful study may be briefly referred to. In the first place, the intensity of the motor nervous impulse cannot be gauged by the magnitude of the resultant muscular contraction, for the latter may be determined by the number of nerve-fibres stimulated rather than by the variability in the intensity of the unit fibre excitation. Lucas, Adrian, Verworn, and others have shown that the intensity of the impulse is not influenced by the strength of the stimulus. In fact, nerves under stimulation behave as muscles do, and exhibit only one degree of activity; it is ' all or nothing.' The strength of the normal stimulus is adjusted by varying the number of fibres in action.

At certain parts in the neuronic or interneuronic tracts there is evidence of a decrement in conduction—for example, at the synapse in the central nervous system, and also in the junctional tissue between nerve and muscle. The decrement in conduction in the nerve-fibre itself has been studied by observing the effects produced by the localised action of narcotics on the nerve-trunk. Among the most interesting phenomena exhibited by nerve in this condition is the rise to the normal intensity of the nervous impulse after its passage through a narcotised area, which is too short to give rise to complete disappearance of the impulse. The progression of the nervous impulse evidently depends not solely upon the energy supplied at its place of origin, but also upon the energy set free locally by the disturbance itself, as in the firing of a train of gunpowder. The chemical changes, however, accompanying the disturbance are so slight as to be difficult of detection. There is evidently a consumption of oxygen and evolution of carbonic acid. The passage of the nervous impulse leaves behind it a condition in which the nerve is temporarily refractory (*fatigue*) to a second stimulus, followed by a period of partial recovery and subsequently by one of increased excitability. The phenomena of summation and inhibition are exhibited by peripheral as well as by central conduction.

The Neurone Doctrine.—It is only within the last thirty years that it has been possible to understand the elements concerned in the working of the nervous system, not only in respect of their structure, but also their function. That the nervous system consisted of fibres and nerve-cells had long been known, that the cells were capable of nourishing the fibre was shown years ago by the experiments of Waller on the dorsal roots of the cord, but there was still something lacking. The origin of the nerve-fibres was unknown, while the distribution of the cells in the grey substance did not appear to be made on any system with a physiological basis. The doctrine of the neurone supplies what was wanting. A neurone is a nerve-cell with its various processes and nerve-fibres. The cell-body,* the fibre, and the processes are a physiological unit, a nervous system in miniature; myriads of such microscopic systems constitute the nervous system.

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* 'The Conduction of the Nervous Impulse,' by Keith Lucas, 1917. Monographs on Physiology.'

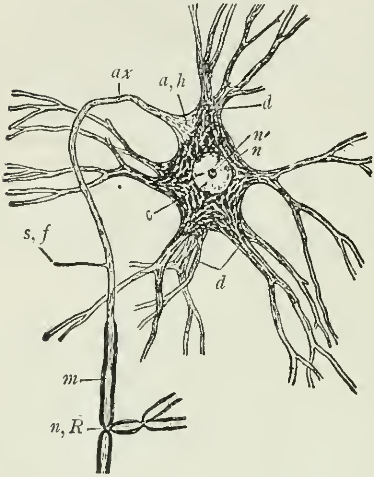

FIG. 133.—STRUCTURE OF MULTIPOLAR CELL (BARKER).

ah, Axon hillock (the portion of the cell from which the axon comes off), containing no Nissl bodies, and showing neuro-fibrils; *ax*, axis cylinder or axon; *m*, medullary sheath, outside of which is the neurilemma; *c*, cell-substance (cytoplasm), showing Nissl bodies in a lighter ground substance; *d*, protoplasmic processes or dendrites containing Nissl bodies; *n*, nerve-cell body or *perikaryon* ; *n′*, nucleolus; *nR*., node of Ranvier; *s.f*., collateral fibril.

A **nerve-cell** consists of a mass of protoplasm intersected by fine fibrils known as *neurofibrils*. Towards the centre of the cell is a refractile nucleus, and lying between the neurofibrils are certain peculiar bodies, which, though granular in nature, stain with methylene blue—an exception to the general staining reactions of cell granules (Fig. 133). These bodies are known as *Nissl's granules*, or *chromophile substance ;* they exist in the form of angular-shaped masses or rods, and extend into all the processes of the cell, excepting that from which the nerve-fibre arises. These granules are intimately concerned in the nutrition of the cell and its fibre, but whether as fluid or granules is unknown. In a working cell the granules diminish, and under great muscular exertion they may be reduced to fine particles, resembling dust in appearance. This is due to the chromophile substance breaking up; the chromatolysis so produced also occurs when the cell is separated from its fibre. It is evident from this that nerve-cells, unlike nerve-fibres, are capable of fatigue. Nerve-cells are not all of the same shape, size, or general arrangement; some have only two processes growing from the cell, and hence are called 'bipolar cells'; other cells have numerous processes, and are called 'multipolar.' All the processes of a nerve are not nerve-fibres; of all the processes in the multipolar cell shown in Fig. 135, only one is the beginning of a nerve-fibre. It is called the **axon**; it is the process of the cell which transmits the impulse. The other processes are called

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* The '*nerve-cell body*' and the '*nerve-cell*' are not the same; the latter includes the dendrites and axons—it is, in fact, the neurone. The former is the cell which gives birth to the neurone, and it is best distinguished as the *perikaryon*.

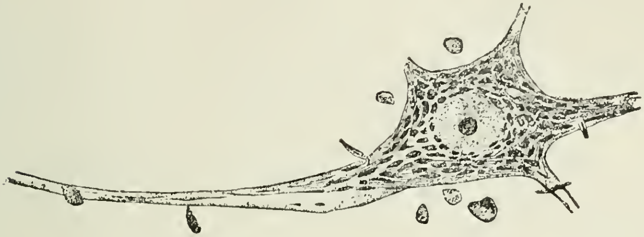


FIG. 134.—CELL FROM THE NUCLEI OF THE OCULO-MOTOR NERVE OF THE CAT (BARKER, AFTER FLATAU).

The nucleus, nucleolus, and Nissl bodies are shown on a larger scale than in Fig. 133.

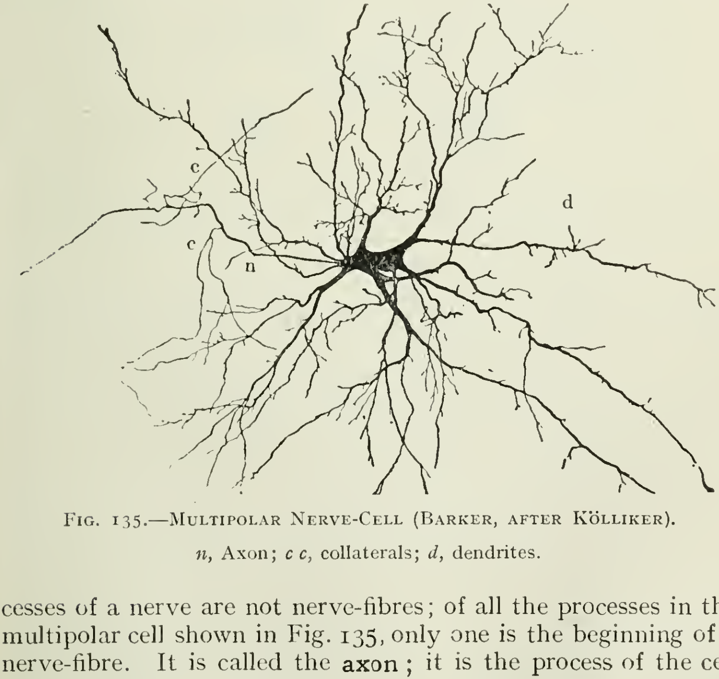


FIG. 135.—MULTIPOLAR NERVE-CELL (BARKER, AFTER KÖLLIKER).

n, Axon; *c c*, collaterals; *d*, dendrites.

dendrites; they are the receiving portion of the cell. The actual conducting materials in the cell are the neuro-fibrils previously spoken of. These pass from the dendrites of the cell into the cell-body, and from the cell-body they pass into the axon. The axon is therefore merely a bundle of neuro-fibrils, a nerve is the immensely elongated process of a nerve-cell. Cells with these processes vary in type and arrangement, but may be classified into the two groups previously mentioned of bipolar and multipolar. **Bipolar cells** are found typically in the ganglia on the roots of the spinal and cranial nerves. These cells are peculiar, inasmuch as they possess no dendrite process. The axon issues as a single process from the cell, and then divides **T**-shaped into two fibres (see Fig. 136); such cells would have been called one-poled, but for the fact that they are known by embryological studies to be bipolar. This type of cell is especially associated with the sensory nerves, and the axon is accordingly long, and may extend, say, from the foot to the spinal cord. The **multipolar cells** (Plate I., 3, and Fig. 135) are more widely distributed, and are found in the grey matter of the brain and spinal cord. They are furnished with processes and the usual axon, but the axon may be long or short, and this peculiarity enables multipolar cells to be divided into two groups, known as Golgi cells of the first and second type. Golgi cells ot the first type may have an actual or relatively long axis cylinder. It may be a cylinder reaching from the cerebrum to the medulla, which would be relatively long, or from a segment of the spinal cord to the foot, which would be actually long. This type of cell is associated with motor nerves. Golgi cells of the second type possess a short, widely-branched axon, which never leaves the grey matter; this type of cell may be seen in the cerebrum and cerebellum. Their short, widely-branching axons lead to the belief that such cells are distributive in function.

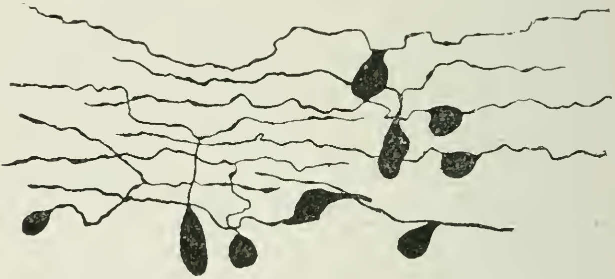


FIG. 136.—CELLS FROM THE GASSERIAN GANGLION OF A DEVELOPING GUINEA-PIG.

The originally bipolar cells are seen changing into cells apparently unipolar. The same process occurs in the cells of the spinal ganglia (Van Gehuchten).

The processes leading to a cell are called **dendrites** (Fig. 135). Some cells, like the bipolar, have no such processes; the multipolar, on the other hand, may be richly endowed. The neuro-fibrils found in the cell extend into it from the dendrites. The function of the dendrites is to collect impulses for transmission to the cell. The remaining process belonging to a cell is termed the **axon** (Figs. 133 and 135); it is the process which gives origin to the nerve-fibre, and into its substance the neuro-fibrils from the cell-body pass. Before the axon of a nerve becomes a nerve-fibre it gives off slender branches known as **collaterals** (Fig. 135); they may be few in number or numerous, as in the case of Golgi cells of the second type. A nerve-fibre terminates by ending in a fine tuft of branches in the neighbourhood of another cell; the tuft is termed *arborisation*, and the junction thus formed with the neighbouring cell is termed a **synapse** (Fig. 138). It is believed that in the neighbourhood of synapses there exists a receptive substance, possessed of certain physiological properties, which favours the transmission of impulses to the neighbouring cell, with which, it will be observed, it does not come into actual contact.

A nerve-cell, its dendrites, axon, collaterals and synapse, constitute a neurone. A **neurone** is a nervous system in miniature; millions of such placed end to end, like the links in a chain, and side by side, like a series of chains, enable the nervous system to be visualised. Some of the links are short, others, we have seen, are long, but no link—*i.e.*, no single neurone—runs from the brain to the periphery of the body. The majority of the neurones originating in the brain extend no farther than the nearest cell station, such as the basal ganglia or medulla; as a rule, either in one or the other, or in both of these places, the neurone ends by arborising around a cell in a ganglion, and a fresh neurone is formed. Even when it gets into the cord it has not necessarily a long run; it may run the length, but the majority of the cord neurones do not; they dip into the grey matter at intervals, and arborise around cells from which fresh fibres arise. This may or may not be the last cell station; if it is the last, the axon passes out into a peripheral nerve, but even when outside the spinal cord a fresh break may occur—as we shall see in dealing with the sympathetic system—a further arborising around cells in the sympathetic ganglia, and finally new fibres. This is what is meant in speaking of the neurones being arranged end to end like the links of a chain. In the simplest conceivable form of nervous mechanism the smallest number of neurones is two; it is seldom that any such simple number exists in the body mechanisms; as a rule, there are several breaks between the periphery and the brain, or the brain and the periphery. A single motor cell in the cerebrum, with its axon, is not connected with a single spinal motor neurone; the latter may be connected with many such cerebral neurones. The sum of all the fibres in the white substance of the brain is, therefore, obviously larger than the sum of those in the cord.

The conducting path is always from dendrites to cell, and from cell to axon. In a neurone a stimulus can be transmitted only in one direction—*i.e.*, from dendrite to axon, so that the dendrite is the receiving portion of the cell, the axon the issuing or distributing portion. No matter how many neurones the impulse has to pass through, nothing is lost excepting time. The impulse is delayed, but it is carried from the termination of the axon across unoccupied fields to the nearest dendrites, and so transmitted to the next cell. There is no *contact* of the cellular elements of one axon with those of another. This is an essential part of the neurone doctrine. There is everywhere contiguity, but no structural continuity.

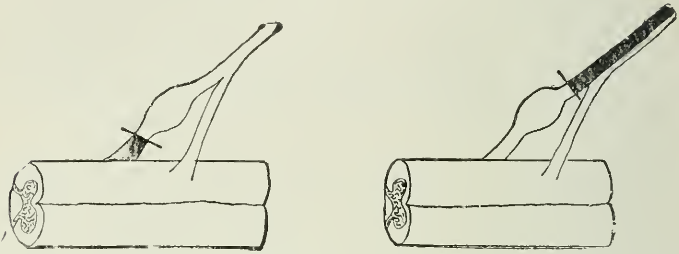
Such is the principle of structure existing in the nervous system, brain or spinal cord, afferent or efferent nerves, cerebro-spinal or sympathetic. There may be variations, and here and there the general rules of construction may be slightly departed from, but the principle is maintained—a principle which explains not only the anatomical, but the physiological side of the system, and enables the mind to grasp the unity of construction of the entire nervous system.

The cell is the life of the fibre. If the fibre be cut off from the cell, it degenerates. Nor is the nutritional change confined to the fibre. The cell also suffers in consequence of loss of function, there being no impulses transmitted to it by its dendrites. The neurone concept consists in regarding the nerve-cell, its dendrites, its collaterals, axon, and terminal arborisation as a physiological unit. Innumerable such units, never touching, but yet brought closely together, constitute the nervous system.

Degeneration and Regeneration of Nerves.—The cell nourishes the axon; if, therefore, the axon be cut off from its cell, degeneration occurs, and this law applies to all cells cut off from their nucleus. We shall see presently that the great inflow and outflow of nerves from the spinal cord is divided into groups—afferent and efferent—broadly speaking, sensory and motor. Every axis cylinder is a nerve, and has a cell-station. In the case of the sensory nerves the cell-station is the ganglion on its root just outside the spinal canal; in the case of the motor fibres the cell-station is in the ventral course of the grey matter of the cord. If a spinal sensory nerve be divided below the ganglion, the whole length of nerve below the ganglion, being cut off from its cell-station, degenerates. If the nerve be divided above the ganglion, those fibres which enter the cord from the **T** division of the two-poled cell alone degenerate, for it is only these which are affected by division above the ganglion (Fig. 137, 1). If the efferent or motor roots be divided, the cell-station being then above the division—viz., in the grey matter of the cord—the nerve degenerates downwards (Fig. 137, 4). If both roots of the spinal nerves be divided below the level of the spinal ganglion, both nerves degenerate in a downward direction (Fig. 137, 3). These profoundly interesting facts, discovered many years ago by the late Dr. Waller, are known after him as **Wallerian degeneration.** By this method of observation it became possible to trace the afferent paths in the spinal cord in consequence of the degeneration produced when these were divided above the ganglion.

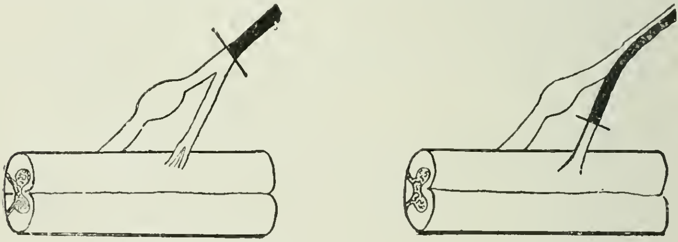
The nerve-fibre, as has been stated above, is but a branch of a nerve-cell. If a portion of a cell be separated from the part containing its nucleus, it soon dies. Thus, when a large amœba, or a Radiolarian, is torn up into several pieces, the portions containing no nucleus degenerate and die; but that portion containing the nucleus repairs itself and re-forms a perfect cell. The nerve-fibre dies down after being cut, just in so far as it is a piece of cell cut off from its nucleus. The sensory nerve divided in neurectomy, as practised on the horse, degenerates towards the foot, and not up the limb, for it is the part below the wound which is cut off from its nutrient centre, and not the portion above. Had this been a motor nerve, the degeneration would still have taken place below the wound, and for the same reason. All spinal nerves have their seat of nutrition either in the spinal cord or in the ganglia just outside it. The nearer to the spinal cord the point at which the section is made, the greater the length of nerve which degenerates; the farther away from the cord the point at which section is practised, the shorter the length which degenerates. When the nerve-degenerates, the fatty medullary sheath breaks up, forming globules around the axis cylinder. The latter also degenerates and ultimately breaks up. The remarkable fact about these changes is the rapidity with which they occur, especially in the dog. Four days is sufficient to show their commencement. Small nerve-fibres degenerate more quickly than large.

The microscopical changes occurring in degeneration are very characteristic. In medullated nerves the axis cylinder swells and breaks up, and the medullary sheath disintegrates into droplets of myelin. Each detached piece of these undergoes a similar change, until the nerve is represented by a bundle of connective tissue without axis cylinder or medullary sheath (Fig. 129, II, III). Along the course of the degenerating fibres proliferation of the neurolemma nuclei takes place to form a scaffolding for the regeneration process. In non-medullated nerve, degeneration is characterised by the disappearance of the axis cylinder. The nerve above the seat of division, though still in communication with the cell, undergoes a limited degeneration as the result of injury, and even the nerve-cells which are intact undergo temporary atrophic changes in consequence of their axons having been cut (Nissl degeneration).



No. 1.—Degeneration of afferent fibres caused by a section of superior root above the ganglion.

No. 2.—Degeneration of afferent fibres following a section of superior root below the ganglion.



No. 3.—Degeneration of efferent and afferent fibres following a section of the entire nerve.

No. 4.—Degeneration of efferent fibres following a section of inferior root.

FIG. 137.—DIAGRAMS TO ILLUSTRATE WALLERIAN DEGENERATION OF NERVE ROOTS (WALLER).

The black portions indicate degeneration.

By the suturing of divided nerves union is established, and though the act of division causes degeneration, yet, when union has taken place, regeneration of fibres occurs. A fresh axis cylinder grows through the length of the degenerated nerve, and after some months motion or sensation is perfectly or imperfectly restored. Sensation is always much later in appearing than motion. After union of severed cutaneous nerves vasomotor tone is recovered sooner than the sensory functions, or the tone of the other smooth muscle innervated tissues—sweat glands and hair follicles. Even suture of divided nerves is not always necessary for union. It is known clinically that the plantar nerves of the horse will often unite in a few months, in spite of a piece having been excised, the portion of nerve above sending down an axis cylinder, which soon finds out the divided portion below. If the gap between the divided ends of a nerve is considerable, a new axis cylinder cannot find its way across.

Trophic Nerves.—Not only is the nutrition of the nerve itself affected by nerve division, but also the nutrition of those parts supplied by it. Ulceration more or less severe has been known to follow injury of certain nerves. Sloughing of the cornea occurs in animals when the ophthalmic division of the fifth is divided, but this may be due to other causes than loss of trophic influence; and many practitioners are acquainted with the sloughing of the entire foot which sometimes, though fortunately rarely, follows the operation of neurectomy. It thus appears that nerves influence the nutrition of a part. It is also well demonstrated in cases of intense muscular atrophy due to nerve injury, and in the dry papillated condition of the nose of the dog after division of the cervical sympathetic. The existence of special trophic nerves has been denied—*i.e.*, of nerves exclusively devoted to maintaining the nutrition of the part. But sloughing of the hoof occurring a few days after neurectomy is evidence of the existence of some special nutrition having been cut off through division of the afferent fibres. The rapid degeneration of muscle after nerve injury is also suggestive of special trophic nerves; the muscles of the scapula or of the hind-quarter of the horse appear to 'melt' away, so rapid in the atrophy.

SECTION 2.

Reflex Action.

Nerve-fibres do not under ordinary circumstances generate impulses; they transmit them, but without modifying them. Modification can occur only in nerve centres, such as the brain and spinal cord, and these centres always consist largely of nerve-cells, of which, as we have seen, the nerve-fibres leaving or entering the centre are simply processes or branches. The spinal cord may be described, not as one long centre, but as a series of centres lying end to end, each capable to a greater or less extent of acting independently of its neighbour, and each centre possessing its afferent and efferent roots.

In these segments of spinal cord complex acts can be initiated by the arrival of simple afferent impulses. Such acts may be carried out without any assistance from the brain, for they can readily be demonstrated in an animal in which the brain has been destroyed. These acts are known by the name of '**reflex**,' from which it must not be inferred that an afferent impulse is simply reflected into an efferent channel, but rather that an afferent impulse reaches the cord, and, passing into the grey matter, stimulates the ganglionic cells which generate the efferent impulse. The structures necessary for a simple reflex act are—(1) an afferent nerve to convey the impression to a nerve-centre; (2) a nerve-centre in which the outgoing impulses are generated; (3) an afferent channel for their transmission (Fig. 138). More complex acts may need a greater number of afferent nerves, of excitable centres, and of efferent fibres. Such a nervous chain is known as a **Reflex Arc**, and can never consist of less than two neurones.

A classical example of a reflex act is exhibited when a frog from which the brain has been entirely removed draws up its leg when the foot is pinched. According to the degree of pressure applied to the foot, it draws up either one leg or both—*i.e.*, the reflex movements are unilateral or symmetrical, according to the number of ganglionic centres in the cord which have been stimulated. Still greater violence applied to the foot of this brainless frog will affect a larger number of centres farther forward in the cord, so that the fore-limbs may share in the reflex. The brainless frog reacts more regularly to this experiment than one possessing a brain, which is evidence that the brain is capable of exercising a controlling influence or inhibitory effect upon reflex actions. One very prominent feature of a reflex act is its apparently purposeful character. An opportunity for studying this in detail will be given presently when the 'reflex frog' is considered.

In the dog very characteristic reflex actions occur after division of the cord, such as those of walking, running, scratching, micturition, and defæcation; and some of these will shortly be considered in detail, owing to their deep physiological importance. The higher the animal scale is ascended, the less easy is it to obtain evidence of free spinal reflexes—viz., reflexes which take place without any guidance from the brain. This may perhaps be due to a more constant influence exercised over them by the brain. Nevertheless, animals as highly developed as the horse and ox give most undoubted evidence of reflex spinal acts. If the spinal cord of either be severed behind the medulla, a cut

The parts within the dotted line lie within the grey matter of the nerve centre.

Re, *Re*, Receptive surface, in this case the skin, impressions from which are conducted by afferent fibres, *dd*, *ax*, to a nerve centre, *pk′*, where outgoing impulses are generated; these are conducted by an efferent channel, *ax′*, to a discharging body, *Ef*, in this case muscle.

The figure is also employed to illustrate conduction and transmission of impulses along a nerve arc. The dotted line encircles a nerve centre (in this case the spinal cord); *dd* then become dendrites on their way to the perikaryon (see note, p. 466), *pk* (in this case the ganglion on the dorsal root of the spinal nerve), or if the perikaryon be short-circuited, the impulse passes direct to the axon, *ax*; this constitutes the *neuronic path*. *sy*, *sy* are synapses, by which the impulse is conducted to the next neurone, through the medium of dendrites, *dd′*, *dd′*, and thence to *pk′*, the cell-body or perikaryon; this constitutes the *synaptic path*.

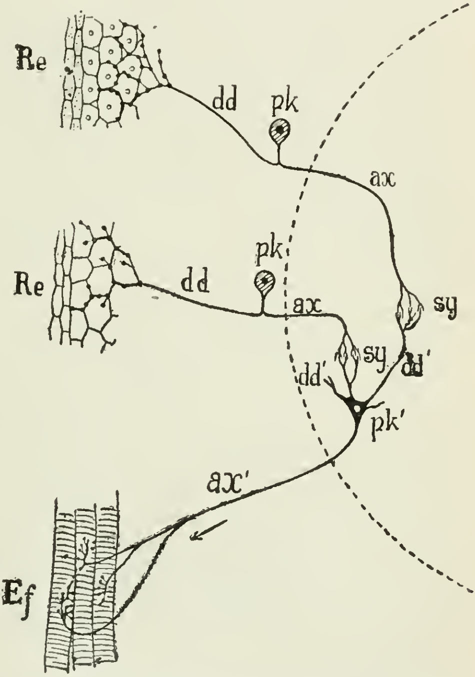


FIG. 138.—DIAGRAM OF A REFLEX ARC (SHERRINGTON).

on the skin of the abdomen will evoke a kick. The excitability of the cord lasts for a few minutes after death; in the ox it lasts longer, but no comparative observations have as yet been made.

Locomotion is often essentially a reflex act. The exact grouping of muscles, and the regulation of the degree and rapidity of their contraction, would appear at first sight to need the supervision of the highest centres in the brain; but this is not the case. A pigeon will fly after decapitation; a brainless dog can walk, and a headless cat, under appropriate stimulation, flexes and extends its legs alternately. If a horse thought of every step he had to take, he would soon be worn out and blunder. That the higher centres also come into play is shown by the judgment which the animal exercises when jumping—viz., he estimates the proper distance at which to take off, the amount of muscular contraction required to lift the body, and the height to which it should be raised. Locomotion, however, is not purely a reflex act, as it is carried out with the knowledge and consent of the animal, but it functions as such. A true reflex act is involuntary, and carried out without the knowledge of the animal.

By a **Co-ordinate Movement** is meant one in which the contraction of various related groups of muscles is so adjusted that the degree of their contraction and everything necessary for a perfect movement is present and faithfully carried out. Co-ordination of movement may occur without the assistance of the brain. In the spinal cord, therefore, not only reflex but co-ordinate movements are generated. The crossed or diagonal movements of locomotion in quadrupeds are of this nature, and are carried out by the spinal cord. Movements which are irregular and purposeless, or in any way fail to co-ordinate, are termed **inco-ordinate.** We shall see later that the co-ordination of muscles is a complex reflex mechanism. All reflex actions are co-ordinate.

The Reflex Frog.—It is usual to illustrate reflex action by reference to the decerebrated frog. In this animal the spinal cord is capable of carrying out the most complex reflex acts, far higher in character than are exhibited by animals with a greater nervous development. If a decerebrated frog be placed in water, it swims; if it be stroked, it croaks; if stimulated, it springs; if placed on its back, it recovers its normal position; if acid be applied to the right thigh, the left foot will be employed to wipe it off, or if this be held, the right leg is flexed. Still more remarkable is the fact that if a brainless frog be placed on a board which is gradually brought from the horizontal to the vertical position, the animal gradually crawls up and, when the board is vertical, sits at the top. If the board be lowered to the horizontal, the creature descends. It is beyond the belief of a layman that such acts are not of a purposive character. As a matter of fact, they fall within the definition of a true reflex act.

If a headless frog be lightly stimulated on one hind-leg, a reflex contraction of the limb occurs; if the stimulus is made stronger, both limbs react. By increasing the strength of the stimulus the fore-limbs may be involved, so that there is a proportion between the magnitude of the reflex acts produced and the strength of the stimulus. There is a latent period in a reflex act (see p. 493), and with each successive increase in the strength of the stimulus the latent period becomes longer in consequence of a greater length of cord being involved. If the frog be injected with strychnine and stimulated, convulsive movements occur, and sensitiveness to touch is greatly increased, so that even a current of air will cause muscular contraction. In this case it is supposed that there is an overflow, as it were, into all motor paths, the strychnine breaking down the barriers which usually direct the impulse. The strychnine does not open new paths, but it converts inhibitory effects into excitatory, so that contractions appear in muscles at the moment they should under normal conditions relax. Incidentally, the sensitiveness shown by the strychnine preparation demonstrates that there are sensory paths leading to all the motor neurones of the body.

The inhibition of reflexes is an extremely important question, which will receive separate consideration.

The reflex acts exhibited by the higher animals are more complex than those of the lower. The normal actions of the latter are almost entirely reflex, whereas those of the former are normally reflexes controlled, modified, or set free, as the case may be, by cerebral centres. If in the dog the cord be divided in the anterior thoracic region, the animal becomes paralysed, there is loss of sensation as well as of motion; yet in process of time recovery occurs, and the isolated portion of cord is capable of carrying on the reflex acts of micturition, defæcation, impregnation, parturition, scratching, and stepping, without the knowledge of the animal. Such a dog may even be able in course of time to walk or run. In the first instance it learns to stand, then takes a few steps before subsiding, and gradually the reflex paths are educated to the new condition which has arisen Locomotion, we have stated, is not normally a true reflex act, yet under purely reflex conditions it may be carried out for hours. The horse has not to think of the order in which he uses his four legs, and how each step is to be taken; the fact is that this is carried out by the spinal cord without the knowledge of the animal; in other words, the work is done for him. It is only when judgment must be exercised or instructions issued that the higher centres take any share in locomotion.

There are movements which may be excited in the limbs after death in both horse and ox, but particularly in the latter, which remind one very strongly of the reflex frog. If immediately after a horse is destroyed an attempt be made to open the abdomen the animal kicks. Some minutes must be allowed to elapse before the irritability of the cord disappears. In the ox the period is longer, and even after decapitation the apparently purposeful movements are very remarkable. For these reasons we believe the cord plays in these animals a more independent part in locomotion than is generally considered. How largely locomotion is reflex may be indicated by the walking of the chick out of the egg. A volitional act requires some experience and training; a reflex act is innate, and may be complete at birth.

Impulse Paths.—When an impulse enters the cord—and it can gain entrance only by the dorsal spinal roots—it may be dealt with locally by a single spinal segment; it may be distributed by several local segments; or it may pass the entire length of the cord and be dealt with by the cerebellum or cerebrum (Fig. 145, A and B). The strength of the entering stimulus may determine whether one or more segments of the cord are involved, as we have seen in the strychnine experiments on the reflex frog. Such a spreading of impulses is termed *irradiation*, and at one time it was believed that this could occur only in a forward direction. Sherrington showed that it could also occur down the cord, though it remains limited to certain lines. We may here trace the path of an impulse, selecting any spinal reflex act. What is true for this is true for all impulses passing to the cord by afferent nerves, and the principle is equally true for those, like sight, hearing, etc., which do not communicate with the cord, but pass direct to the brain. We have seen that a reflex arc (Fig. 138) consists of a chain of nerve-cells, each complete link being called a 'neurone,' the neurones following each other end to end like the links of a chain; further, that a complete neurone is made up of a nerve-cell body (perikaryon*) with its processes, some of these, the dendrites, being the receiving and another, the axon, being the transmitting process. We also know that the axon terminates by arborising around the dendrites of the next link. The passage of an impulse in a nerve-arc must lie during part of its course within the neurone (in all cases travelling from dendrite to axon, though not necessarily traversing the perikaryon, which may be short-circuited). Having arrived at the end of one neurone, the impulse has then to cross the space existing between it and its neighbouring neurone; the region in which this occurs is the synapase. Conduction is therefore in part *within* the neurone or intraneuronic, shortly *neuronic*, and in part *between* the neurones, interneuronic or preferably *synaptic*, as it occurs in the area of a synapase (Fig. 138). The whole of the conduction and transmission of impulses in the nervous system then become describable as (1) neuronic and (2) synaptic, and this distinction is physiologically fundamental, because the nature of the conduction cannot be the same in the two cases. In all nerve-centres synaptic conduction is added to neuronic conduction; synaptic conduction is irreversible in direction, neuronic conduction is reversible.

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* See footnote, p. 466.

The **Receptor System** has been revealed by the work of Sherrington; it is a system engaged in the transmission of impulses from the periphery to the centre. It forms the basis of the classification of afferent nerves on p. 454. The impulses are received in what he has termed 'fields of distribution,' and of these there are two main divisions—*surface* and *deep*. A surface field may be external, or *exteroceptive*—for example, the skin—or internal (*interoceptive*), such as the mucous membrane of the nostrils. The deep field, or *proprioceptive* system, lies in the muscles, joints, tendons, viscera, etc. Whereas the surface field is brought into operation by its surroundings, such as touch, pressure, heat, cold, sight, hearing, smell, the deep field is activated by something derived from itself—for example, mass, weight, pressure or alteration of pressure, such as occurs in a contracting or relaxing muscle. The first step, then, in the conveyance of an impulse—say, from the skin to the cord—is that the nerve-path shall originate in a *receptive field*. An area of skin consists of points forming a receptive surface, from which the nerve-path starts. The receptive neurone extends from the receptive surface to the central nervous organ, and it is the sole avenue which impulses generated at its receptive point may use, no matter whither they may be proceeding or how distant their destination.

A single receptive point may play reflexly upon a number of different effector organs—*i.e.*, organs connected with the efferent system, muscles, glands, and suchlike—yet all its reflex arcs spring from the one single shank—viz., from one afferent neurone, which conducts from the receptive point at the periphery into the central nervous organ. This neurone dips at its deep end into the spinal cord or brain, and in this network forms manifold connections. So numerous are its potential connections that, as shown by the general convulsions induced under strychnine-poisoning, its impulses can discharge every muscle and effector organ in the body. Yet under normal circumstances the impulses conducted to the central network do not irradiate in all directions. Their spread, as judged by the effects produced, increases with increase of stimulation of the radiant path, but the irradiation remains limited to certain lines. Under weak stimulation these lines are few. The conducting network offers, therefore, to any given path entering it, some communications that are easier than others. This is sometimes expressed by saying, borrowing from electrical terminology, that the conductive network from any given point offers less resistance along certain circuits than along others. This recognises the fact that the conducting paths in the great central organ are arranged in a particular pattern. This pattern reveals something of the integrative function of the nervous system. It shows us what organs work together in true relationship. The impulses are led to this and that effector organ, gland or muscle, in accordance with the pattern.

The receptive neurone forms, as we have seen, the sole avenue by which impulses generated at its receptive point can be conveyed to their destination. It is a path exclusive to the impulses generated at its own receptive points, and receptive points other than its own cannot use it. The receptive neurone forms a **private path** exclusively devoted to impulses from a single receptive point. Our study of the skin has shown that its entire surface is a collection of receptive points. On reaching the cord the impulses pass along certain *association* tracts or *internuncial* paths—*i.e.*, paths which connect the various segments of the cord. These are paths common to groups of private paths, and at their terminations the impulses pass from the synapses across the space which separates these from the first link or neurone in the chain of the efferent path. The efferent path passes out, in the case of the cord, by the ventral spinal nerves to the gland or muscle concerned, where it terminates in a final neurone. The motor or efferent path differs in one important respect from the sensory or afferent, inasmuch as it is not exclusively devoted to the transmission of impulses generated at a single receptive source, but receives impulses from many receptive sources situated in various regions of the body. It is, however, the sole path by which all impulses, no matter whence they come, must travel if they would reach the muscle, gland, etc., concerned. It is a **public path** common to impulses of all kinds, such as tissues are constantly receiving. Reflex arcs arising, therefore, in different sense-organs can pour their influences into one and the same muscle. A limb-muscle is the *terminus ad quem* of nervous arcs arising not only in the right eye, but in the left; not only in the eyes, but in the organs of smell and hearing; not only in these, but in the otic labyrinth, in the skin, and in the muscles and joints of the limb itself, and of all the other limbs as well. Its motor path is a nerve common to all these arcs. It is the **final common** path, and a motor nerve to a muscle is a collection of such final common paths.

The afferent neurones comprising the private paths are several times more numerous than the common paths; in other words, the outlet is much smaller than the inlet, and in consequence there is competition for the right of way. In this matter there is no compromise in a conflict, say, between two opposite reflexes. One or the other must pass, both cannot. We shall see this well illustrated in the 'scratch' and 'foot reflex' of the dog. The victory in this struggle lies, as usual, on the side of big battalions. The stronger the stimulus, the more likely is it to occupy the road, especially if it be of a painful nature. The stronger inhibits the weaker. The weaker is not necessarily destroyed; it may simply be held back, and permitted to follow when the stronger rival has left the road open. Inhibition does not take place in the motor nerve itself. The field of competition between the rival arcs seems to lie in the grey matter, where the converging neurones come together at the commencement of the common path, and here it is that some arcs force the final path into one kind of action; others force it into a different kind of action; and others, again, preclude it from being employed by the rest. In studying the reflex act of stepping, we will see this feature well illustrated in the reciprocal innervation of antagonistic muscles. We have previously learnt (p. 436) that while the flexor muscles of a limb are contracting the tone of the extensor muscles is inhibited; this inhibition arises in the nerve-centre, the stream of motor impulses along the motor neurone being for the time cut off in the struggle for the common path. This fact is of the utmost importance to a clear understanding of the question of muscular co-ordination, and further consideration of the question will be given later.

On the receptive surface the various impressions, such as light, touch, heat, cold, taste, smell, and so forth, are selected by the special afferent nerves devoted to their transmission. The spinal connections of different nerve-endings in the same area of skin are assumed to be different, since stimuli suitable for one set of movements are unsuitable for another. The scratch reflex needs tickling or stimulation of a hair for its production. The reflex of the 'extensor thrust,' which has yet to be spoken of, can only be excited by pressing between the plantar cushion and the toe-pads of the dog, and no other form of stimulation can invoke it. A consideration of the special spinal reflexes now to be described will prove object-lessons in the principles of the common path, and the remarkable mechanisms it is capable of effecting.

The Stepping Reflex.—In the dog, when the spinal cord has been severed in the hinder part of the cervical region, and the 'shock' from the transection has passed off, reflex walking is observable. The walking movement includes alternate flexing and straightening of the limb. The forward movement of the hind-leg in taking a step is produced by flexion at the hip, and to prevent the foot brushing against the ground as the leg swings forward flexion occurs at the stifle and hock, so as somewhat to raise the foot. The limb is then straightened again, so that the foot may reach the ground and bear the weight of the body. In order to prevent the limb doubling up under this burden, the extensor muscles which support the patella joint and hock from bending have to contract with sufficient power. Stiffened by the contraction of these muscles, the limb serves as a prop to support the body. While the foot rests on the ground the body moves forward, so that in due course the hip advances in front of a vertical drawn upward from the foot. The extended hind-limb at this time is sloped somewhat backward as well as downward. When this posture is reached, the extensor muscles are thrown into further action, and give the limb a push off from the ground, propelling the body forward. The hind-limb thus makes its contribution to the forward progression of the body; in galloping in the normal dog this *extensor thrust* is very marked.

In this reflex spinal stepping we may study first the flexion of the limb which occurs in the forward movement of the step. Flexion similar but more pronounced can be easily excited in the *spinal dog** by exciting the skin of the foot electrically. Though the flexion occurs at hip, patella joint, and hock together, it will be simpler to confine our examination to the flexion at one of these joints only, for what occurs in the muscles of each of the three joints is, so far as concerns us now, the same. The chief muscles which flex the stifle are the *semitendinosus* and *biceps* at the back of the thigh. The electric stimulation of the skin of the foot is found to throw these muscles into contraction, and, with them, also the *psoas* muscles (flexors of the hip) and the *tibialis anticus*, etc. (flexors of the hock). But this is only part of what happens. At the same time as the flexors of the stifle contract, the extensor muscles of the stifle, the *vasti* and *crureus*, are relaxed. The same stimulus which excites the motor neurones of the flexors to discharge motor impulses into those muscles causes the motor neurones of the antagonistic muscles, the extensors of the stifle, to cease discharging impulses, and keeps them prevented from discharging impulses. The stimulus sets up an intraspinal *excitation* of the motor neurones of the flexor muscles and an *intraspinal inhibition* of the motor neurones innervating the extensor muscles.

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* 'Spinal dog' is the term used to indicate that the reflexes are entirely spinal, owing to the brain having been destroyed, or the cord having been cut off from the brain.

When the flexion phase of the act of stepping has been passed through, the leg extends again by return of the activity which had been inhibited in the motor neurones of the extensor muscles. In due course the foot reaches the ground. When it does so the weight of the body gradually comes upon it, and presses the sole of the foot hard against the ground. A stimulus is thus given to nerve-endings in the sole. This stimulus can be imitated—for instance, by pressing against the toe-pads with a finger. This, in the spinal dog, even when the animal is lying on its side, excites a strong reflex extension of the limb, the '**extensor thrust.**' Just such an extension occurs when the foot is pressed against the ground by the weight of the body in the act of stepping. This extensor thrust gives the propulsive forward movement of the body, which is the contribution made by the limb in its reflex step toward the progression of the animal. The extensor thrust is particularly marked in the gallop.

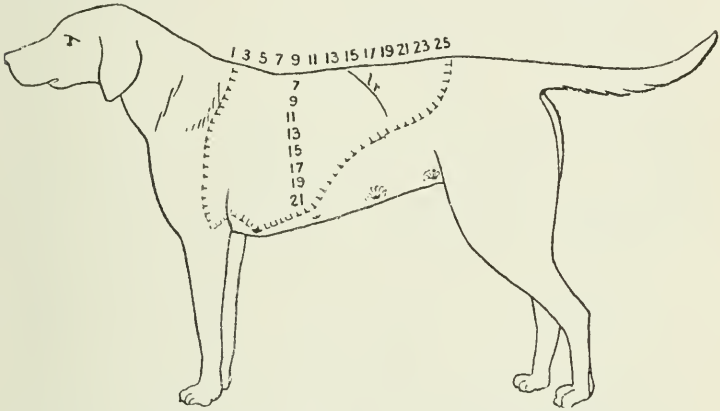

FIG. 139.—THE SCRATCH REFLEX (SHERRINGTON).

The 'receptive field,' as revealed after low cervical transection, a saddle-shaped area of dorsal skin, where the scratch reflex of the left hind-limb can be evoked. *lr* marks the position of the last rib.

The Scratch Reflex.—Good opportunity for study of this correlation between reflexes is given in the 'scratch reflex.' This reflex can be easily elicited in many normal dogs; when the spinal cord has been transected in the neck, it becomes abnormally responsive. Stimuli applied within a large saddle-shaped field of skin (Fig. 139) excite a scratching movement of the leg. The movement is rhythmic flexion at hip, stifle, and hock. It has a frequency of about four per second. The stimuli provocative of it are mechanical, such as rubbing the skin or pulling lightly on a hair. The nerve-endings which generate the reflex lie in the surface layer of the skin, about the roots of the hairs. A convenient way of exciting these is by feeble faradisation.

Prominent among the muscles active in this reflex are the flexors of the hip. If we record their rhythmic contraction we obtain tracings, as in Fig. 141. A series of brief contractions succeed one another at a certain rate, whose frequency is independent of that of the stimulation. The contractions are presumably brief tetani. The stimulus to the hair-bulbs of the shoulder throws into action a lumbar spinal centre, innervating the hip-flexor, in much the same manner as the bulbar respiratory centre drives the spinal *phrenicus* centre. In the case of the respiratory muscle the frequency of the rhythm is, however, much less.

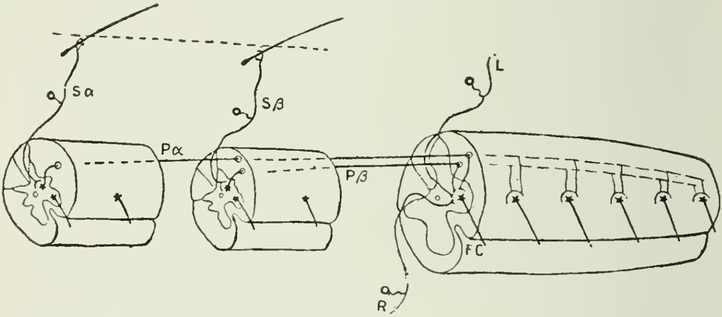

Fig. 140.—Spinal Arcs involved in Scratch and Foot Reflexes (Sherrington).

Diagram of the spinal arcs involved in Fig. 139. L, Receptive or afferent nerve path from the left foot; R, receptive nerve-path from the opposite foot; Sα, Sβ, receptive nerve-paths from hairs in the dorsal skin of the left side; Pα, Pβ, neurones originating within the cord; FC, the final common path, in this case the motor neurone (nerve-path) to a flexor muscle of the hip.

The reflex is unilateral: stimulation of the left side of the back evokes scratching by the left leg, not by the right. In the lateral column of the spinal cord fibres exist directly connecting the spinal segments of the shoulder with the spinal segments containing the motor neurones for the flexor muscles of the hip, and stifle, and hock. We thus arrive at the following reflex chain for the scratch reflex: (1) The receptive neurone (Fig. 140, Sα), from the skin to the spinal grey matter of the corresponding spinal segment in the shoulder. This is the exclusive or private path of the arc. (2) The long descending neurone within the cord (Fig. 140, Pα), from the shoulder segment to the grey matter of leg segments. (3) The motor neurone (Fig. 140, FC), from the spinal segment of the leg to the flexor muscles. This last is the *final common path*. The chain thus consists of three neurones. It enters the grey matter twice—that is, it has two neuronic junctions, two synapses. It is a *disynaptic* arc.

Now if, while stimulation of the skin of the shoulder is evoking the scratch reflex, the skin of the hind-foot is stimulated, the scratching is arrested. Stimulation of the skin of the hind-foot causes the leg to be flexed, drawing the foot up. This is the **foot reflex.** The drawing up of the foot is effected by strong tonic contraction of the flexors of hock, stifle, and hip. In this reaction the reflex arc is: (1) The receptive neurone or nerve-path (Fig. 140, L), from the foot to the spinal segment; (2) perhaps a short intraspinal neurone; and (3) the motor neurone or nerve-path (Fig. 140, FC) to the flexor muscle—*e.g.*, of hip. Here, therefore, we have an arc which embouches into the same *final common path* as Sα. The motor neurone FC is a nerve-path common to it and to the scratch reflex arcs; both arcs employ the same effector organ, a hip-flexor.

The channels for both reflexes finally embouch upon the same common path. The flexor effects specific to each differ strikingly in these two cases. In the scratch reflex the flexor effect is an intermittent contraction of the muscle; in the foot reflex it is steady and maintained. The accompanying tracing (Fig. 141) shows the result of conflict between the two reflexes. One reflex displaces the other from the common path. There is no compromise. The scratch reflex is pushed aside by the reflex arc provoked from the foot. The stimulation which previously sufficed to evoke the scratch reflex is no longer effective, though it is continued all the time. But when the stimulation of the foot is discontinued the scratch reflex returns.

This remarkable result indicates that there is interference between the two reflexes, and that one has inhibited the other. Though there is no cessation of activity in the motor neurone, one form of activity that was being impressed upon it is cut out and another has taken its place.

Suppose, again, during the scratch reflex, stimuli are applied to the foot, not of the scratching, but of the opposite side (Fig. 140, R). This stimulation of the foot causes flexion of its own leg and extension of the opposite. If, therefore, when the left leg is executing the scratch reflex, the right foot is stimulated, the scratching is cut short, though it is the left leg's flexors which are involved. This inhibition of the flexor scratching movement occurs sometimes when the contraction of the extensors is minimal or hardly perceptible.

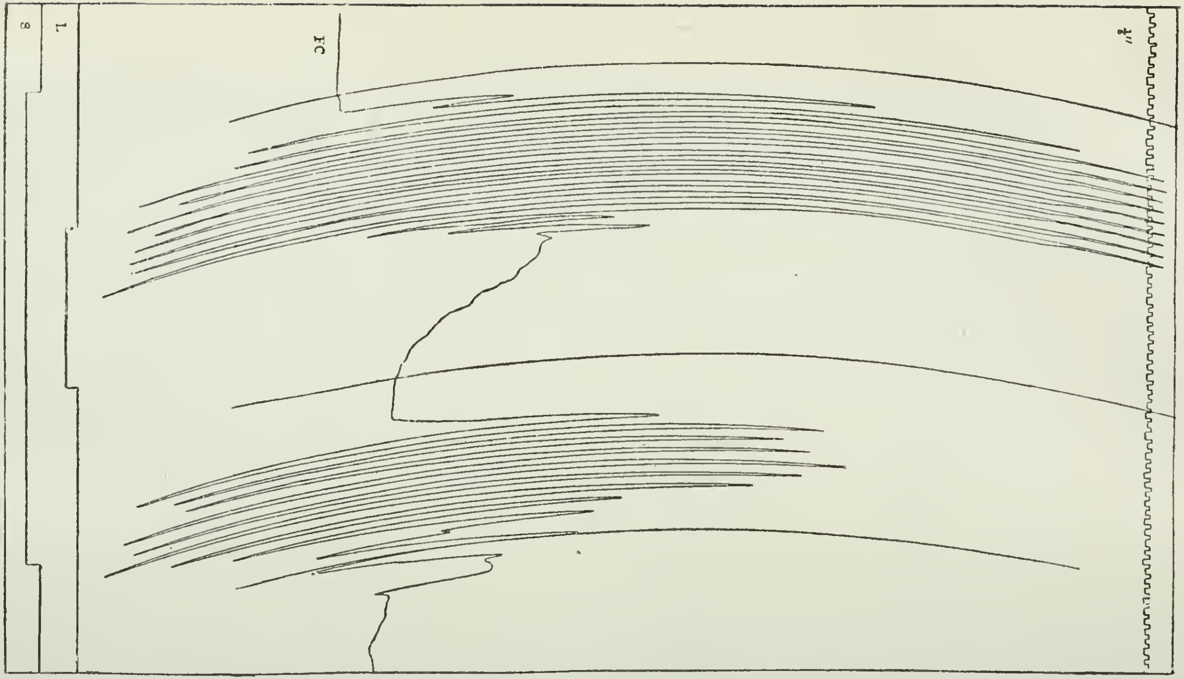

FIG. 141.—THE RESULT OF CONFLICT BETWEEN THE SCRATCH AND FOOT REFLEXES.

Stimulation of the dorsal skin (Fig. 140) induced the scratch reflex FC, which begins at the notch in the signal line S, and continues throughout the period of that notch. Later, for the period marked by the notch in signal line L, the stimulation of the foot is made. This latter stimulation interrupts the clonic scratch reflex in the manner shown. The time is registered above in fifths of seconds. The tracing reads from left to right. It is noteworthy that the interruption of the scratch reflex by the foot reflex is not established directly the foot stimulus begins, and that it outlasts for a short time the application of the foot stimulus.

It is obvious from this that the final common path, FC, to the flexor muscle can be controlled by, in addition to the beforementioned arcs, others that actuate the extensor muscles, for it can be thrown out of action by them. The final path, FC, is therefore common to the reflex arcs, not only from the same side foot (Fig. 140, L) and shoulder skin ($S\alpha$, $S\beta$), but also to arcs from the opposite foot (R), in the sense that it is in the grasp of all of them. In this last case we have a conflict for the mastery of a common path, not, as in the previous instance, between two arcs, both of which use the path in a pressor manner, although differently, but between two arcs that, though both of them control the path, control it differently, one in a pressor manner heightening its activity, the other in a depressor manner lowering or suppressing its activity.

We said that the scratch reflex is unilateral. If the right shoulder be stimulated, the right hind-leg scratches; if the left shoulder be stimulated, the left hind-leg scratches. If both shoulders be stimulated at the same time, one or the other leg scratches, but not the two together. The one reflex that takes place prevents the occurrence of the other. The reason is that, although the scratch reflex appears unilateral, it is not strictly so. Suppose the left shoulder stimulated. The left leg then scratches. If the right leg is then examined, it is found to present steady extension, with some abduction. This extension of the leg which accompanies the scratching movement of the opposite leg contributes to support the animal on three legs, while it scratches with the fourth.

Suppose now we stimulate the left shoulder, evoking the scratching movement of the left leg, and that the right shoulder is then appropriately and strongly stimulated. This latter stimulus often inhibits the scratching movement in the opposite leg, and starts it in its own. In other words, the stimulus at the right shoulder not only sets the flexor muscles of the leg of its own side into scratching action, but it inhibits the flexor muscles of the opposite leg. It throws into contraction the extensor muscles of that leg. In the previous example there was a similar coordination. The motor nerve to the flexor muscle is therefore under the control not only of the arcs of the scratch reflex from the shoulder on the same side, but of those from the opposite shoulder as well. But in regard to their influence upon this final common path, the arcs from the homonymous shoulder and the opposite shoulder are opposed.

The scratch reflex occurs in many animals besides the dog—*e.g.*, the cat, guinea-pig, sheep, rabbit, rat, parrot. In small animals its rate of rhythm is greater than in large; the scratch is quicker in small dogs than in large.

The Falling Reflex of cats is a well-known reaction. A fully inverted cat, if allowed to fall, alights squarely on all four feet. The reflex is not abolished by the destruction of the motor areas in both hemispheres of the cerebrum, but ablation of both hemispheres prevents it from occurring. The phenomenon is dependent on influences from the semicircular canals of the internal ear and eyes, controlled by the cerebral cortex, for though destruction of the labyrinths does not prevent the reflex, this follows when the eyes are occluded.

The Pinna Reflex.—By gently twisting the tip of the pinna of the ear of the cat a reflex is elicited consisting of a quick retraction and folding back of the pinna. The motor nerve is the seventh cranial, while the second cervical nerve contains the afferent fibres. It is also observed in the decerebrate preparation.

The Head-Shake Reflex.—By blowing into the ear of the cat a rotatory shake of the head is caused; it can also be observed in the decerebrate preparation, the occipital stump rotating. A few drops of water introduced into the concha produces the same effect. The reflex is protective to the auditory meatus, the left ear producing a shake in the direction of the hands of the clock, the right ear reflex being anti-clockwise.

Tendon Reflexes.—One of the best known of the tendon reflexes in man is the knee-jerk, a jerking forward of the leg when the straight ligament of the patella is struck. This is caused by a momentary single spasm of the extensor muscles of the knee, due to a sudden pull on the muscle when the tendon is tapped; this excites the afferent nerves within the muscle, and a reflex response through the motor nerves follows. It is well seen in the dog, cat, rabbit, etc. It is dependent on the reflex tonus that is maintained in the muscles by the spinal arcs connected with them; if that tonus be much lowered, as by severance of the nervous reflex arc, the jerk can no longer be elicited. Sherrington describes the knee-jerk as the prototype of the *proprioceptive* class of reflexes. Another brisk 'jerk' in the dog is the *ischial*, obtained from the hamstring muscles by tapping the tuberosity of the ischium.

Tendon reflexes have not, so far as we are aware, been studied in the horse; nor is it known whether the existence of any limb reflexes has been demonstrated, if, perhaps, we except the immediate lifting up of the foot, which generally follows pinching the so-called 'chestnut' found on the inside of the fore-arm of the horse.

Reflex Inhibition.—In the reflex movements of 'stepping' and 'scratching' in the spinal dog, attention has been drawn to acts of inhibition; for instance, it was shown that the stimulus which excites the flexors to contract causes the extensors to relax. The stimulus to produce contraction in the extensors is still present, but it is inoperative, owing to inhibition. It was also shown that the scratch reflex, having been started on one side of the body, could be inhibited by starting it on the opposite side. In this case the stimulus starts one set of flexor muscles going, and inhibits the corresponding set of flexors in the opposite limb. Similarly, in the conflict between the two reflexes of scratching and stepping, all the conditions needful to maintain the scratch reflex in operation are present, but they are inhibited so long as the pad of the foot is pressed upon; when that stimulation is withdrawn, the scratch reflex returns. We have therefore to consider the question of *reflex inhibition.*

The visceral muscles receive, as we have already seen, a double efferent nerve-supply. The heart muscle and that of the intestines and bloodvessels can be stimulated or inhibited; this is effected by one efferent conveying impulses of an excitatory character, while the other efferent conveys inhibitory impulses. These work reflexly under the control of an afferent service, and the nature ot the impulses in the afferent determines which of the efferent impulses are to be placed in operation. Muscles, as we have seen, are provided with an effective afferent system of nerves, more than half the fibres belonging to a muscle being of this nature. Sherrington has shown that where the muscle passes into the tendon, a ‘ nest of afferents ’ exists, and he has also proved that the Golgi organ found in tendon is afferent in nature. In spite of this liberal afferent system, there is only a limited efferent outflow; muscles are well supplied with nerves conveying excitatory (motor) impulses, but there are no nerves conveying inhibitory impulses. Notwithstanding, inhibitory functions in skeletal muscle are of a most important and widespread character, and they are effected in a purely reflex manner by inhibiting the neurone which conveys the excitatory impulses.

Under the title of **reciprocal innervation** Sherrington describes what occurs in all normal movement—*i.e.*, a relaxation of antagonistic muscles. For instance, while the flexors of a limb are contracting, their antagonists, the extensors, are relaxing. This effect is brought about by the tonus (p. 436) of the antagonistic muscles being reduced, owing to an inhibition of those motor cells in the cord which supply the extensor muscles. Reciprocal innervation thus saves a waste of nervous energy in overcoming the contraction of antagonists, and it insures muscular co-ordination. In certain muscular movements antagonistic muscles may contract concurrently. This is evident in those cases where a muscle is connected with two or more joints, being a flexor of one and an extensor of another. In this case antagonistic muscles are capable by their contraction of inhibiting the extensor movement of one joint in order to permit the muscle to act as flexor of another. The innervation of the antagonistic muscles so employed is no longer reciprocal, but identical, as they must contract and relax at the same time, and not alternately.

The purposes served by reflex inhibition in skeletal muscular actions are classified by Sherrington as follows:*

1. Reflex inhibition cuts short the contraction of one set of muscles when another set is called into play; it also guards and maintains a reflex already in operation by preventing its being interrupted by other stimuli

2. It grades the degree of intensity of the discharge from nerve centres by diminishing it to any required extent, so that the needful discharge from a motor centre can be adjusted with the greatest precision.

3. Reflex inhibition exhibits itself in respiration, stepping, eyeball movements, and the reciprocal innervation of antagonistic muscles, the underlying principle being that by means of reflex inhibition the contraction of a muscle causes relaxation of its antagonist.

4. Inhibition is the main means by which rhythmic reflexes are produced. For example, the rhythmic reflex in stepping being excited, its execution produces a stimulus which brings into activity a reflex inhibition; this cuts the rhythmic reflex short. The muscle having ceased to contract, the inhibition is removed, and the original stimulus is once more in undisputed possession of the field, and so rhythmicity is maintained.

5. On the withdrawal of inhibition, there is a great augmentation of activity in the inhibited centre. This Sherrington describes as **post-inhibitory rebound**; this rebound favours the change from flexion to extension, and *vice versa*. He regards it as responsible for one of the two phases of such diphasic muscular reflexes as stepping, mastication, and respiration. It is evident that when one or more pairs of legs are concerned in locomotion, some of the limbs are in a condition of flexion, the others are in extension; and the change from one phase to the other is brought about by post-inhibitory rebound.

6. Strychnine converts reflex inhibition into *reflex excitation*, and the toxins of tetanus and rabies have the same effect. These agents, as pointed out by Sherrington, 'work havoc' with the elemental co-ordination of the skeletal muscles, changing reciprocal innervation into identical innervation. Hence, in tetanus patients, the greater the effort to open the jaw, the more tightly is it closed; and in the hydrophobia patient, the greater the attempt made by the sufferer to inhibit his inspiration in order to swallow, the deeper and more prolonged the inspiration which ensues, inhibition 'being converted by the virus into excitation.'

7. Chloroform and 'fatigue' strengthen inhibition. An inhibitory reflex stimulus, which is ineffective on a normal centre when that centre is fresh, becomes effective when the centre is under chloroform, or when the active driving of the centre has been pushed for a little time.

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* 'The Rôle of Reflex Inhibition,' *British Medical Journal*, March 25, 1911, and *Science Progress*, No. 20, April, 1911.

In complex reflexes many stimuli are at work together, and co-operate harmoniously for a co-ordinate result. In standing, walking, running, etc., very important sources of the reflex lie in the muscles and joints of proximal parts of the limb—namely, in the joints of the hip and stifle and the great muscles acting on them. These joints and muscles are liberally supplied with afferent nerves. The importance of these as sources of the reflex of stepping is indicated by several facts. In the first place, a dog or cat is found still to walk well when the foot reflex is cut off in all four feet by division of the nerves, both superficial and deep. In the second place, when the spinal dog is lifted so that its limbs do not touch any solid support whatever, reflex walking and galloping are performed, although the limbs are stepping wholly in the air. But to excite this reflex of walking in the air, it is necessary that the limbs hang down. The reflex ceases if the dog be inverted, when gravity is no longer acting on the joints and muscles as it does in the position usually accompanying acts of stepping. It is evident that impulses which stimulate contraction are passing from muscles and joints to spinal centres. The spinal centres which execute reflex walking, running, etc., receive much help and direction from afferent arcs which arise in the labyrinth ot the ear. The stimuli which are the source of reflex walking, etc., arise, therefore, in many receptive organs.

It is by means of the deep stimuli that the proprioceptors of the limbs maintain the extensor muscles in a state of tonic activity, and so enable the upright position of the body to be maintained without effort and without the knowledge of the individual. When, therefore, the spinal dog is held in the air legs downwards, gravity acting on the joints and muscles—namely, weight and pressure—is the cause of impulses passing from the deep fields to the spinal cord, and so maintaining the act of stepping. When the animal is inverted, the deep fields no longer receive their natural stimulus, and the movement ceases. We shall see shortly that the chief ganglion controlling the *proprioceptive system* is the cerebellum.

The Standing Reflex.—When the brain of a dog or cat is removed between the anterior and posterior *colliculi*,* the extensor muscles of the limbs, the extensor muscles of the neck, back, and tail, and those which close the jaw, are in a condition of mild tonic contraction. Their antagonists, the flexors, exhibit relaxation. The phenomenon is known as **Decerebrate Rigidity.** The rigidity of the extensor muscles is due to impulses passing out from the cord as a reflex effect, for if the afferent nerves of the muscles be divided the rigidity ceases. The reflex effect originates in the muscle, for if the nerves of the skin be divided the rigidity continues. The decerebrate preparation, if stood on its legs, remains there, the rigidity of the extensor muscles of the abovenamed parts sufficing to maintain the erect attitude, even for days at a time. When, however, the brain stem is divided behind the pons the preparation can no longer remain erect, nor can a decapitated dog or cat stand.

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* The term ‘ colliculi ’ is now used to denote the *corpora quadrigemina*. Its shortness is convenient, and it avoids confusion in the case of reptiles, birds, fish, etc., where these structures are bigeminate.

An animal, when standing, is frequently altering its pose (see p. 435); we have learned that this is effected by the lengthening and shortening contraction of the extensor muscles, by which means the muscle, though counteracting the same load—namely, the weight on the limb—can adjust itself at different lengths. There are also modifications of posture effected through the influence of the otic labyrinth and deep afferents of the neck. If the head of the *decerebrate preparation* be flexed, the fore-quarters sink owing to inhibition of the extensor muscles of the fore-legs, while there is increased tension of the extensors of the hind-quarters; the posture assumed by the body resembles that seen in the horse when 'stretching.' If the head be tilted upwards and backwards, the fore-quarters are raised owing to contraction of the extensor muscles, while the hind-quarters sink, the final attitude resembling that assumed by a horse when in the act of rising from the ground, or a cat looking up at an object. When the head is turned to one side, as in the familiar posture adopted by a horse when looking round in his stall, the extensor muscles of the fore and hind limbs on the same side of the body exhibit increased extensor action, while on the opposite side of the body there is a decrease in the extensor effect. The influence of the labyrinth in relation to the position of the body in space will be referred to again in the chapter on the senses.

Other Reflex Acts.—We have seen that reflex acts are not confined to skeletal muscles; the act may be secretory or nutritive, or one involving the contraction or relaxation of pale muscle; for example, the contraction and dilatation of the bloodvessels under the influence of the vasomotor system, the peristaltic movements of the intestines, the contractions of the bladder and uterus, the movements of the pupils, and the secretions from various glands, are all examples of reflex acts.

Reversal of Reflex Effect.—The influence of the nervous system in regulating as a reflex effect the calibre of the bloodvessels has been dealt with elsewhere (p. 86). It is not proposed to refer again to this, excepting to illustrate a phenomenon known as reversal of reflex effect. When an ordinary afferent nerve is stimulated in the dog, the effect produced on the bloodvessels is that of constriction, and the blood-pressure is reflexly raised. Bayliss has shown that a rise in pressure can be converted into a fall by a sufficient dose of chloroform. In observations by Sherrington and Sowton on skeletal muscle, it was found that the excitatory reflexes brought about by strychnine could be undone by chloroform or ether, so that the reflex response could be changed back from contraction to inhibitory relaxation, and on permitting the chloroform narcosis partially to pass off, the strychnine influence reappears. In the decerebrate preparation the above observers showed that reflex contraction of skeletal muscle or reflex inhibition could be produced at will through the same afferent nerve by varying the strength and form of the electrical stimulation, and in other ways. Instances begin to be numerous in which the reflex obtainable from one and the same afferent nerve may be diametrically reversed on alteration of some one definite factor in the conditions of the reaction.

Peripheral Reflex Centres.—Centres for reflex action outside the brain and spinal cord have long been carefully looked for, especially in connection with the sympathetic system. So far as is known, there are no sympathetic acts purely reflex; nor are all the necessary structures present in the sympathetic system for the formation of a reflex arc. The ganglia on the dorsal roots of the spinal nerves are similarly structured, and they are not seats of reflex action. We have seen that a reflex arc requires an afferent nerve, a centre, and an efferent nerve. All three of these are not present in connection with a sympathetic or spinal ganglion.

The **Time occupied by a Reflex Act** varies dependently upon the strength of the stimulus and the nature of the reflex; the sharper the stimulus, the more immediate the reflex; the more active the centre, the more rapid the response. Impulses which have to cross the cord take longer to produce their effects than those which enter and return from the same side. It is mainly during this appreciable delay, or latent period, as measured by delicate apparatus, that the changes which lead to an efferent response are occurring in the grey substance. In the dog the time occupied by a reflex on the same side is estimated at from 0·022 up to 2-3 seconds, according to circumstances.

SECTION 3.

Spinal Cord.

The spinal cord extends from the atlas to about the second or third sacral vertebra, and is completely enclosed in a dense membrane, the dura mater. The canal in which it is lodged is very much larger than the cord, especially at those parts where the greatest amount of movement occurs, as in the neck. The cord is not the same shape nor the same size throughout; oval in the cervical region, it becomes circular in the dorsal, and again oval in the lumbar portion. It is largest where any considerable bulk of nerves is being given off, and thus there is an enlargement corresponding to the fore, and another to the hind limbs (Fig. 142). On exposing the spinal canal, a large number of nerves are found to be passing through the dura mater either outwards or inwards, and these gain an exit from or entrance to the spinal canal by means of the foramen formed at the junction of the vertebræ.

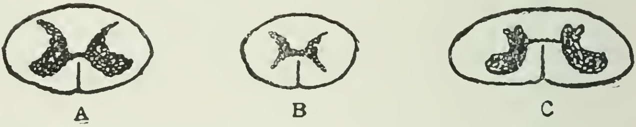

FIG. 142.—TRANSVERSE SECTION OF SPINAL CORD OF HORSE.

A, At level of first dorsal vertebra; B, at level of first lumbar vertebra; C, at level of first sacral vertebra.

Spinal Nerves.—These are given off from or enter the cord from the first bone of the neck to the fourth or fifth sacral vertebra. A bunch of nerves passes through every intervertebral foramen on each side, and these represent the spinal nerves. When the dura mater of the cord is opened, it is observed that the nerves within this cover are arranged in two groups: one derived from the dorsal, the other from the ventral, aspect of the cord. These are the superior and inferior roots of the spinal nerves, or, to maintain the preferable nomenclature, the dorsal and ventral roots. In the horse the dorsal and ventral roots leave the cord, not as a single bundle, but as several. On the dorsal root a nodule is found where the nerve passes through the intervertebral foramen. This is the spinal ganglion, and as the roots are in bundles, so there are bundles of ganglia at each outflow between the vertebræ (see Fig. 145). There are no ganglia on the ventral roots. Dorsal and ventral roots unite outside the intervertebral foramen to form the ordinary mixed spinal nerve. The functions of these two roots are quite opposite. In the dorsal roots the impulses are passing from the periphery to the centre; they are afferent fibres, and from the fact that they convey impulses which give rise to sensations of various kinds, they are also known as 'sensory.' In the ventral roots the impulses are passing from the centre to the periphery; they are efferent nerves, and, from the fact that the majority of the efferent impulses result in movement, they are also known as 'motor' nerves. A portion of cord embracing a pair of spinal roots is spoken of as a segment, and the spinal cord consists of a series of such segments united end to end.

Passing away from the spinal cord in company with the ventral roots is a branch known as the *white ramus communicans.* So soon as it gets outside the vertebræ it leaves the ventral root and passes to a portion of the nervous system known as the 'sympathetic.' The sympathetic system is frequently regarded as a something quite distinct from the ordinary cerebro-spinal system, and in function this is very largely true; but the white ramus communicans serves to remind us that the two systems are very closely linked, and are under one central authority. It is unnecessary here to follow the white ramus farther; it will be fully considered with the sympathetic system.

Function of the Spinal Nerves.—If the dorsal spinal roots be divided, all parts supplied by them below the division lose sensation; if the portion of nerve in connection with the spinal cord be irritated, pain is produced. The spinal sensory fibres endow the whole body with sensation, with the exception of certain parts of the face. If the ventral roots be divided, all parts supplied by the nerves below the seat of division suffer motor paralysis; if the cut end of the nerve still in connection with the tissues be irritated, the muscles contract vigorously; while if the piece of nerve in connection with the cord be irritated, nothing happens. In this way it is demonstrated that the sensory impulses pass into, whilst the motor impulses pass out of, the cord. Sometimes pain is felt when the motor roots are divided, due to one or two branches of the sensory nerves finding their way back into the cord by this channel. The phenomenon is known as *recurrent sensibility*.

Columns of the Cord.—If a cord be suitably prepared, a transverse section (Fig. 143) shows it to consist of two similar halves, united by a comparatively small central mass of tissue, through the centre of which a minute longitudinal canal runs. The halves are separated by fissures on the dorsal and ventral surfaces of the cord. The ventral median fissure is wide, and does not reach down to the centre, while the dorsal median fissure is narrow and deep. Each half of the cord is seen to consist of dorsal, lateral, and ventral columns, separated from each other by a shallow longitudinal groove. A section of the cord shows it to be made up of both white and grey matter, the latter, internally placed, forming the medulla. This is arranged something like the letter H, or like two inverted commas placed back to back. The shape of the grey matter on transverse section depends entirely on the region of the cord examined. This may be seen in Fig. 142, which shows three sections of the cord. The dorsal and ventral ends of the comma, or crescent-shaped halves of the grey matter, are spoken of as the cornua. From the dorsal cornu the afferent or sensory fibres run; from the ventral run the efferent or motor roots. The white substance of the cord also varies in thickness (see Fig. 142). Stated generally, the cord increases in white matter from the tail to the head. The grey matter is largest in the cervical and lumbo-sacral enlargements, and this increase and decrease in size corresponds with the

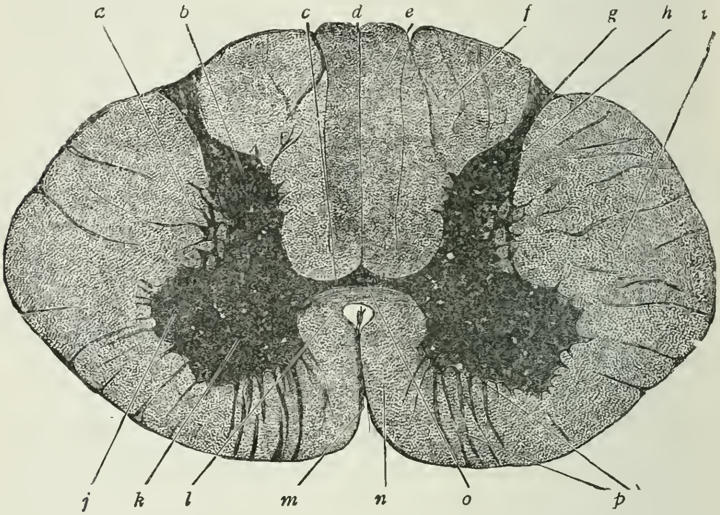

Fig. 143.—Transverse Section of the Spinal Cord in the Cervical Region × 8d. The Lines in the Lateral and Superior Columns running from the Outer Margin are Laminæ of the Pia Mater (M'Kendrick).

a, Processus reticularis; *b*, dorsal horn; *c*, grey commissure; *d*, dorsal septum; *e*, Goll's column; *f*, superior column; *g*, point of entry of dorsal root; *h*, substantia gelatinosa; *i*, lateral column; *j*, large multipolar nerve-cells; *k*, ventral horn; *l*, white commissure; *m*, inferior longitudinal fissure; *n*, inferior column; *o*, central canal; *p*, point of exit of ventral roots.

increase and decrease in the number of nerves entering and leaving the cord in these regions.

The **Grey Matter of the Cord** may be regarded as a pair of long columns extending throughout its length. These columns, when examined microscopically, are found to consist mainly of nerve-cells, some of which are connected with the dorsal, others with the ventral roots of the spinal nerves. A collection of nerve-cells possessing afferent and efferent nerves is essentially a ganglion, and, regarded in this light, the grey matter of the spinal cord may be considered to be built up of a series of ganglia placed end to end and communicating. In the ventral cornu of the grey matter the cells are largest and arranged in groups. The cells, as we have already seen (p. 468), are multipolar; their axons are the origin of the fibres of the ventral or motor spinal root. Every motor nerve obtains its nerve-cell origin in the inferior cornu, and wherever the outflow of nerves is greatest, as in those parts of the cord opposite to the limbs, there these cells are largest and most definitely grouped. There is another group of cells in the ventral cornu which is not connected with the building up of motor nerves; their axons pass from the grey into the white matter, and travel up, down, and across the cord, where they constitute short tracts of white matter, which knit together the various segments. These are known as 'association fibres.' Between the ventral and dorsal cornua is a portion of grey matter known as the 'intermedio-lateral column.' In this part are the cells connected with the nerves which link up with the sympathetic system, and supply the viscera by means of the *white rami communicantes*. The cells in the dorsal horn of the cord are smaller, and the cell-groups not so well marked. There is, however, a group of large cells extending throughout the dorsal grey matter in the thoracic cord, known as 'Clarke's column.' It furnishes fibres which pass into the white substance of the cord, and form there what is known as the *direct cerebellar tract*.

The **White Matter of the Cord** consists of medullated nerve-fibres, generally running longitudinally; structurally, these fibres differ from those found in the body-nerves by the fact that they possess no neurilemma, the medullary sheath being contained within a supporting material known as *neuroglia*. The white matter of the cord is divided into certain columns—dorsal, lateral, and ventral. These anatomical columns give no notion of the physiological paths which exist between the brain, cord, and body. These paths in the white matter have been mainly worked out by the degeneration method—viz., by studying the degeneration which follows division of the spinal nerves. If, for example, cutting the dorsal roots above the spinal ganglion leads to the degeneration of tracts in front of the injury, it is known this must be a sensory or ingoing path; if the degeneration occurs behind the injury, it is evident that the affected fibres have their cell-station farther forward, and that the path is motor or outgoing. Another method of tracing the tracts is the developmental. In the early embryo the fibres have no myelin sheath; when, later on, this appears, it is observed that all the fibres belonging to the same group are simultaneously invested with myelin. In this way it is possible to determine the fibres possessing a common course. There are other methods of inquiry which need not here be referred to; sufficient has been said to indicate the nature and difficulties of this class of investigation.

Paths in the Cord.—The white matter forms paths in the cord, which are spoken of as ascending and descending tracts.*

The ascending and descending tracts in the spinal cord of man have been mapped out only after years of laborious research, in which pathological as well as physiological results have been utilised. In man the tracts are numerous and complex; as the animal scale is descended simplification occurs. The monkey is less complex than man, but more complex than the dog, and so on. Tracts present in man are absent in the lower animals; for instance, a tract known as the *direct pyramidal*, which connects some motor centres in the brain with the limbs and muscles concerned, has no representative outside of man and the higher apes. Another, known as the *crossed pyramidal tract*, and well represented in man and the monkey, is but insignificant in the dog (see Fig. 144). The columns of white matter in the spinal cord of the domesticated animals have not been clearly made out, with an exception to be mentioned presently, and we shall, in consequence, be compelled to refer to the columns in man in order to illustrate the principle on which the work is carried out. The white tracts do not run unbroken throughout the length of the cord; some are long and others short; some disappear for good; others change their relative positions at different levels. Speaking generally, the descending tracts diminish in size from the head towards the tail; the ascending tracts increase from the tail to the head. The shorter tracts are probably the older ones developmentally, for long tracts are more conspicuous in highly developed animals in which the independent activity of the cord is imperfectly retained, while short tracts are associated with more independent function of the spinal cord and less development of the higher centres.

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* These terms have been retained for quadrupeds in preference to the expressions 'headwards' and 'tailwards,' or 'forwards' and 'backwards.'

Descending Tracts in the Cord.—These run from the brain to the spinal cord in the ventro-lateral columns of the white matter, and give off aborisations to the motor neurones of the ventral or motor roots of the spinal nerves (Fig. 145). Most probably there are other descending paths not yet discovered, but those which are clearly known are as follows:

- *Direct Pyramidal Tract.*
- *Lateral Pyramidal Tracts—*
  - (*a*) *Crossed or Hetero-Lateral.*
  - (*b*) *Homo-Lateral.*
- *Rubro-Spinal Tract.*
- *Proprio-Spinal Tracts.*
- *Vestibulo-Spinal Tract.*

Direct Pyramidal Tract.—This is found only in man and the anthropoid apes. It is associated, and the same holds good for the *Lateral Pyramidal Tract*, with complex, skilled, and delicate muscular movements, such as occur in man; it is through these channels that these movements are produced and directed. The more highly developed the brain, the larger the direct pyramidal tract. In Fig. 144 the position and relative size of this tract in man is shown. Both pyramidal tracts are spoken of as *cortico-spinal*, to indicate that they connect the cortex of the cerebrum with the spinal cord.

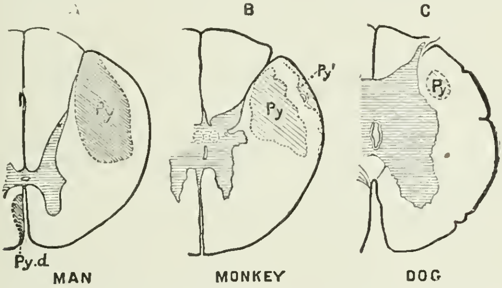

Fig. 144.—Diagram to illustrate the Relative Size of the Crossed Pyramidal Tract (Py) in the Dog, Monkey, Man (Foster, after Sherrington).

In B, Py′ is an outlying portion of the pyramidal tract separated from the rest by the cerebellar tract. Py.d in A is the direct pyramidal tract.

Crossed or Hetero-Pyramidal Tract.—This is the main descending motor path in animals (Figs. 144, C; 145, A). Nevertheless, it is relatively smaller than in man, for the size of this tract bears some relation to the size of the motor areas in the brain. Where these are small, as in the horse, ox, and sheep, the tract is small. Small motor areas suffice for animals such as the horse, where the limb movements are of a simple pendulum type. The combined areas of the two pyramidal tracts in man constitute nearly 12 per cent. of the total cross area of the cord. The following shows the proportion the crossed pyramidal system bears to the cord in other animals:

Cat	7·76 per cent.
Rabbit	5·30 ,,
Guinea-pig	3·00 ,,
Mouse	1·00 ,,
Frog	Absent.

The crossed pyramidal tract is so named on account of its fibres crossing in the medulla on their way to the cord. In the direct pyramidal tract there is no crossing. The effect of the fibres crossing is that the right cerebrum controls the muscles on the left side of the body, and *vice versa*. If an animal be shot in the right brain it falls on the left side, as these muscles are the first to be paralysed.

In the dog, and perhaps in other of the lower animals, there are other paths than the pyramidal conveying impulses which lead to motion, for if all the pyramidal fibres be divided, complete paralysis does not follow, while stimulation of the motor areas of the cerebrum continues to produce muscular contraction. It is believed that the supplemental path is the *rubro-spinal tract*, which takes its origin in the red nucleus of the mid-brain, and is considered by Dexler* to replace in animals the direct pyramidal tract.

J. L. King has investigated the crossed pyramidal tract of the sheep.† He finds it to be imperfectly developed, and that it does not extend beyond the first cervical segment. In the medulla some of its fibres decussate, others are uncrossed. This short tract represents all the motor fibres having origin in the cortex of the cerebrum; from this we should expect that not only are the cortical motor areas small, but that motor fibres must be derived from some other portion of the brain. King has found this to be the case. In the ventro-lateral columns of the cord of the sheep are two well-developed descending paths running its entire length. One of these he identifies as the *rubro-spinal tract*. These two tracts represent in the sheep the chief primary motor paths in the cord. Centrally they are connected with the mid-brain, pons, and medulla. The fibres are consequently subcortical in origin. The two motor paths are reinforced by proprio-spinal fibres, which bring them into intimate relation with near and distant segments of the cord. King concludes that the chief motor paths in the spinal cord of lower mammals do not, as in man, originate in the central cortex, but from a point lower in the brain.

Homo-Lateral Pyramidal Tract.—Some uncrossed fibres lie in the same position as the crossed pyramidal tract.

Rubro-Spinal Tract.—Known also as the *Pre-pyramidal or Monakow's Tract*, lies just below the crossed pyramidal tract (Fig. 145, A). It arises in the mid-brain from the red nucleus. King considers that one of the two well-marked motor paths in the sheep represents the rubro-spinal tract found in some other animals. This tract in the dog is referred to above.

The *Proprio-Spinal Descending Tract*, or tracts, consists of fibres which connect the more anterior spinal segments with the more posterior. The fibres of these in the dog are much more numerous than the pyramidal tract fibres, and their importance lies in the fact that they connect the four limbs together in locomotion.

Vestibulo-Spinal or Ventro-Lateral Descending Tract.—This tract has its origin in one of the vestibular nuclei (Deiters' nucleus). In the cord it lies in the ventro-lateral column near the surface of the cord.

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* 'Veterinary Anatomy,' S. Sisson.

† The *Quarterly Journal of Experimental Physiology*, vol. iv., No. 2, June, 1911.

Ascending Tracts.—These are as follows:

The *Direct or Dorsal Spino-Cerebellar Tract* (tract of Flechsig).
The *Median Superior Tract* (column of Goll).
The *Lateral Superior Tract* (column of Burdach).
The *Ventro-Lateral Ascending or Ventral Spino-Cerebellar Tract* (tract of Gowers).

The *Direct or Dorsal Spino-Cerebellar Tract* (Fig. 145, A) arises in the peculiar group of cells in the grey matter on the inner side of the dorsal horn. The axons from these cells run to the cerebellum without crossing. This tract forms a long afferent path, and it has been made out that the fibres from the lumbar portion of the cord lie outermost; the dorsal fibres lie within these; and, finally, the fibres from the anterior dorsal and lowest cervical nerves are innermost. All the fibres comprising this tract do not reach the brain; many terminate in the cord. The tract terminates in the cerebellum, which it enters by the posterior peduncle.

The *Median Superior Tract* lies on either side of the dorsal median fissure. The fibres composing it are small, and the path terminates at the bulb. This tract is made up of long fibres of the dorsal roots of the tail, pelvis, and hind-limbs, and runs up and ends mainly in the bulbar nucleus of Goll, often called the *leg* nucleus. Degeneration of the tract occurs when the dorsal roots of the cord are divided. In Fig. 145, A, this tract corresponds to the sensory path marked 'hind-leg' and 'tail.'

The *Lateral Superior Tract* is derived from long fibres of the dorsal roots of the thoracic region, fore-limbs, and neck. It runs up and ends mainly in the bulbar nucleus of Burdach (*nucleus cuneatus*) commonly spoken of in man and the monkey as the *arm* nucleus. In Fig. 145, A, this sensory path is indicated by the portion marked 'fore-leg,' 'neck,' and 'trunk.'

The Ventro-Lateral Ascending or Ventral Spino-Cerebellar Tract.—In the case of this tract the precise seat of origin is unknown. Division of the dorsal roots of the spinal nerves produces no effect upon it. Its origin must therefore be within the cord. The tract terminates in the cerebellum, part entering by the anterior peduncle. The fibres terminate by arborising around cells in the middle lobe of the organ.

Association Fibres.—Certain short fibres, previously mentioned, arise in the cord, and form tracts uniting the various segments. They originate from 'tract cells' in the grey matter of the cornua, and from here run into the white substance, but after a short course they run back and re-enter the grey matter. These tracts may be ascending or descending; their function is to knit together the various spinal segments.

The above ascending and descending tracts do not account for the total amount of white matter; there are still unmapped regions in the cord.

When the various ascending tracts reach the medulla, they undergo change in form, position, and distribution. Some, as we have seen, terminate in cells in the bulb; in fact, there are only two upward paths which pass through unbroken—viz., the two cerebellar. All the descending tracts which are passing from the cerebrum to the cord, pass through unbroken.

Functions of the Ascending Tracts.—In the *median superior* and *lateral superior tracts* and in the dorsal columns of the cord

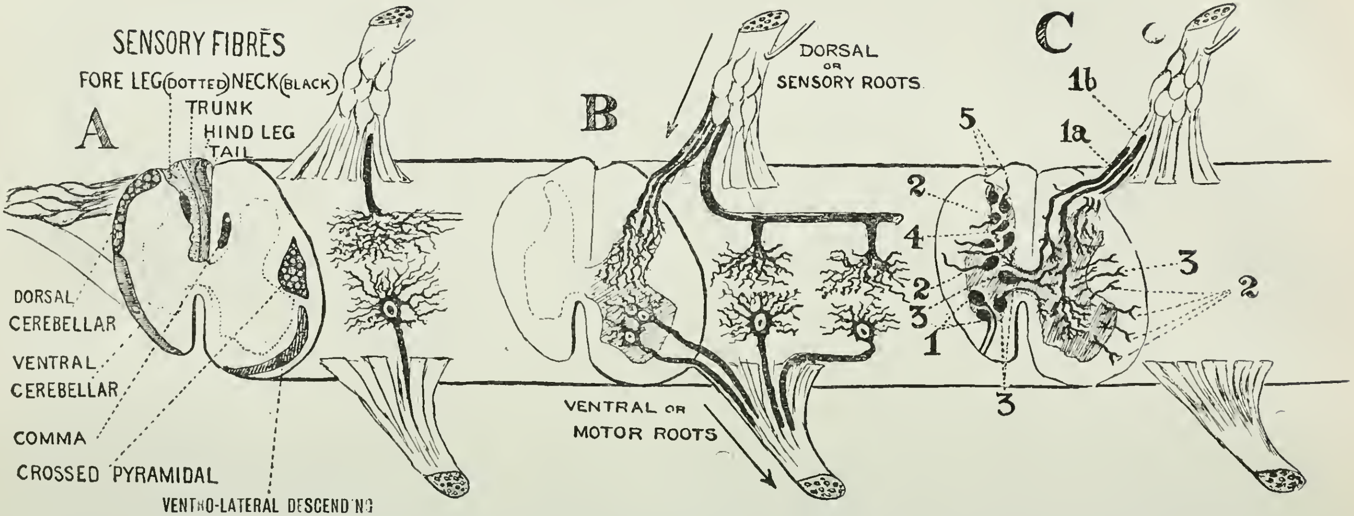
SENSORY FIBRES
FORE LEG (DOTTED) NECK (BLACK)
TRUNK
HIND LEG
TAIL
A
DORSAL CEREBELLAR
VENTRAL CEREBELLAR
COMMA
CROSSED PYRAMIDAL
VENTRO-LATERAL DESCENDING
B
DORSAL OR SENSORY ROOTS
VENTRAL OR MOTOR ROOTS
C
1b
1a
5
2
4
2
3
1
3
3
2

FIG. 145.—DIAGRAM OF THE SPINAL CORD, SHOWING THE STRUCTURAL FEATURES BY WHICH SOME OF ITS PRINCIPAL FUNCTIONS ARE CARRIED OUT.

A is a sectional view of the cord which may be conveniently referred to the cervical region, the head being to the left of the observer. B and C are to be visualised as sectional transparencies.

A

The right segment of the cord, the farther from the observer, shows the *ascending tracts* ; the left segment shows the *descending tracts.*

In the dorsal portion of the right half of the cord is shown the relative position of the sensory root fibres connected with the limbs, trunk, and tail, contained in the columns of Goll and Burdach, that of Goll being nearest to the central line.

In the lateral and ventral columns of the same side are shown the other ascending paths, the *dorsal cerebellar* from Clarke's column of the same side, the *ventral cerebellar* chiefly from the grey matter of the opposite side.

In the left half of the cord are shown the descending or motor tracts. The *comma* tract, not referred to in the text, consists probably only of root fibres in the dorsal column; the *crossed pyramidal* tract is indicated, and below this the *ventro-lateral descending* or *vestibulo-spinal* tract. The dorsal and ventral roots are seen united on the far side, with ganglia on the dorsal roots.

B

The spinal roots are shown as separated. The method by which they enter and leave the cord is indicated, the arrows pointing in the direction taken by the impulses. The mechanism concerned in a simple reflex act is shown diagrammatically, the incoming fibre arborising around cells in the grey matter, the impulse travelling out by the ventral root, or passing up the cord, arborising later, and so passing out. A more complex system consists of another neurone placed between those already shown.

C

In the right segment of the cord are shown the nerve-cells, in the left the entering nerve-fibres.

Right side : (1) *Motor cells* giving origin to the ventral roots; (2) *tract cells*, the axons passing into the white matter of lateral and ventral columns; (3) *commissural cells*, the axons of which cross the cord; (4) *Golgi cells, second type*, the axons of which do not leave the grey matter; (5) *tract cells*, the axons passing into the white matter of dorsal columns.

Left side : 1, *a* and *b*, entering fibres of sensory roots; 1*a*, ending in Clarke's column of same side, and dorsal column of opposite side: 1*b*, sensory fibres arborising around cells of ventral roots of same side. Below 1*b* are fibres to the lateral and superior column of same side. 2 and 3 are collateral fibres, 2 for the ventral and lateral columns, 3 from the pyramidal tract, arborising around motor cells in the ventral portion of the grey matter.

impulses are conveyed which lead to a sensation of pressure (touch), but more especially impressions from skeletal muscles, tendons, and joints, known as *muscle-sense*, to which is due the co-ordination of muscles in locomotion. It will be remembered that the lateral superior tract is almost wholly composed of sensory fibres from the muscles. These impulses are carried up the side of the cord into which they entered. In the bulb the paths end, and fresh fibres are formed, which cross to the opposite side to terminate in the cerebrum, in the area known as that of the *body-senses*. Injury to the fibres of body-sense produces an awkwardness in gait; the animals show a want of skill in using the hind-limbs. The muscles are there, but, owing to the loss of muscle-sense, they are not conscious of them, and consequently are unable to direct their movements.

The *dorsal cerebellar tract* and the *ventral cerebellar tract* carry impulses connected with deep sensibility arising from muscles, tendons, and joints. Each of these tracts terminates in the cerebellum; it is believed they are also associated with muscular co-ordination, which, as we shall see later, is the special function of the cerebellum.

The nerve-fibres which give rise to sensations of pain and temperature after entering the cord end in the grey matter; fresh axons are then formed, which run up both sides of the cord. In the medulla the fibres terminate, and fresh axons arise from its cells, which pass to the optic thalamus of the opposite side. This is the chief station for all varieties of afferent stimuli. In both the ascending and descending paths there are fibres terminating in the cord—*i.e.*, not running the full length of the tract. This is especially the case with the afferent fibres, the larger number of which enter the grey matter, where many terminate by arborising around tract cells. Many tract cells furnish further fibres, which continue the path.

All sensory impulses pass to the brain on the side opposite to their origin, and all motor impulses leave the brain on the opposite side to that to which they are distributed, so that injury to a left motor area leads to a right body paralysis (see Fig. 147).

The termination of the sensory fibres in the cord has been in part referred to. Having passed through their cell-stations in the ganglia on the dorsal spinal nerves, they enter the cord, but do not directly pass along it as an afferent tract, but penetrate the grey matter, where many terminate (Fig. 145, A); others are provided with fresh axons, and then continue the headwards passage as a spinal tract. As a matter of fact, the entry of the fibres into the cord is by no means so simple as the above would suggest, and it is further complicated by the fact that the fibres on entering the cord divide into a **Y** or **T**, one branch passing backwards for a short distance, the other forwards, both, perhaps, giving off collaterals (see Fig. 146). Some of these collaterals establish cell communication with the grey matter, and so with the motor system, a reflex arc being thus formed (Fig. 145, A and B). The reflex arc may be complicated by the introduction of an intermediate set of neurones, connecting the cell termination of the sensory nerve with the cell origin of the motor.

Special Centres in the Spinal Cord.—In the cord certain centres exist, which, though ordinarily under the control of a chief centre in the bulb, yet are capable, as we have seen, of carrying on peculiar reflex actions even after the cord has been divided.

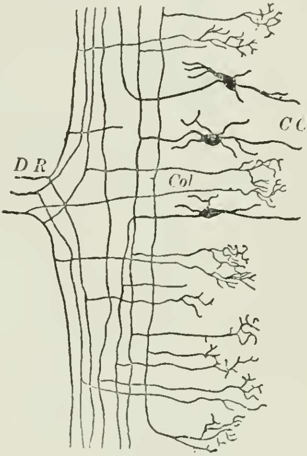

Fig. 146.—Branching of Dorsal Root Fibres in Cord (Donaldson, after Ramon y Cajal).

DR, Dorsal root fibres entering the cord, and dividing **Y**- or **T**-wise into fibres running forwards and backwards, which give off collaterals, *Col*. Cells, *CC*, can be seen in the grey matter of the cord with which the collaterals establish communication.

The *cilio-spinal centre* lies between the cervical and dorsal portions of the cord; in it fibres originate which through the cervical sympathetic supply the dilator muscle of the iris. Destruction of the region in question causes a contraction of the pupil, whilst irritation of it causes the pupil to dilate. The *ano-spinal* centre, found in the lumbar portion of the cord, controls the act of defæcation; it would appear to be highly developed in herbivora, which possess the power of bringing it into play not only when the body is at rest, but during movement. The functions of the ano-spinal centre appear rather complex, inasmuch as it has not only to maintain the tone of the sphincter, but also to relax it during defæcation, and under the latter condition simultaneously to contract the abdominal muscles and diaphragm. These contractions, however, are brought about quite simply through the reciprocal innervation of antagonistic muscles (see p. 489). The *vesico-spinal* centre also exists in the lumbar portion of the cord, and governs micturition; its action is similar to that of the ano-spinal centre. In the lumbar portion of the cord other centres are found—for example, the *erection* centre, the *genito-spinal* centre, which contains the nervous apparatus employed in the emission of semen, and the *parturition* centre. *Vasomotor* centres are found throughout the cord; they are principally under the control of similar centres in the bulb, but may act independently. All these centres in the cord are activated through the sympathetic system.

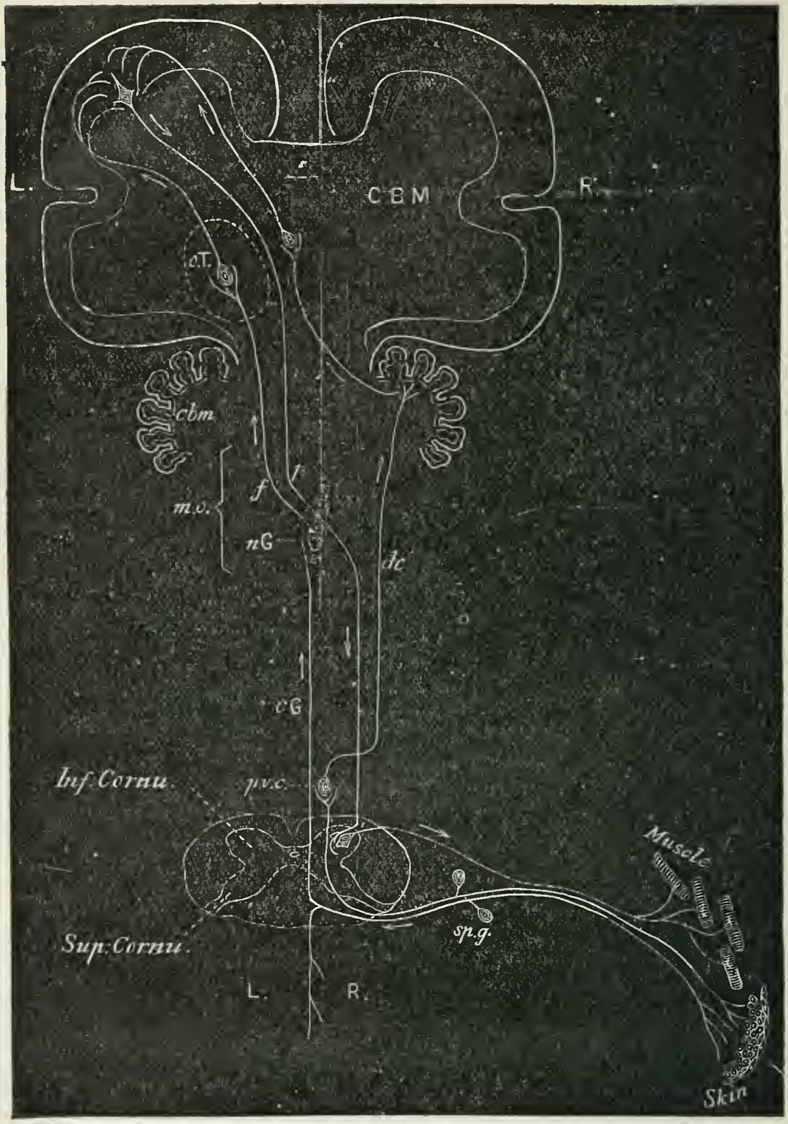

Fig. 147.—Diagram of the Afferent and Efferent Paths passing to and from the Brain by the Cord (Sherrington).

L, Left; R, right; CBM, cerebrum; *cbm*, cerebellum; *mo*, medulla oblongata, containing the decussation of *p*, the pyramidal tract, and of *f*, the fillet; the decussation of *f* should really be a little higher instead of a little lower than that of *p*; *n*G, nucleus gracilis (Goll's); *o*T, optic thalamus; *pvc*, the superior vesicular column, or column of Clarke; *sp g*, spinal ganglion; *c*G, median superior column (Goll's); *dc*, direct cerebellar tract.

The arrows show the direction of the impulses. An afferent impulse, say from the skin, passes along the sensory nerve, through the spinal ganglion, and enters the dorsal columns of the cord; it may pass to the cerebrum direct via the medulla by *c*G, the median superior column, which crosses in the bulb, and so gains the opposite side of the brain; or the impulse may pass by *dc*, the cerebellar tract, to the cerebellum, entering it on the same side, and from here crossing over to the opposite cerebral hemisphere. An efferent impulse originates in the cerebral cortex, gains the pyramidal tract, passes through the bulb to the *opposite* side of the cord, enters the cells in the inferior cornu of the grey matter, and passes out in the inferior spinal nerves. The arrows denote the direction of the impulses.

SECTION 4.

Bulb (Medulla Oblongata), Pons, and Mid-Brain.

The change undergone by the spinal cord in merging itself into the bulb may be studied by successive sections of the latter. Briefly it may be stated that the central canal of the cord widens in order to become subsequently the fourth ventricle; the symmetrical and regular arrangement of the grey and white matter of the cord becomes broken up, not only in order that it may find its way to its destination in the higher centres, but that those fibres which are passing out may be collected from the various outlying centres, and brought together in an orderly manner in the smaller and more compact structure, the medulla. But the medulla is not only a highway for nerve-fibres passing in two opposite directions—it is also a cell centre; and besides restarting all the tracts which terminate in the bulb on their way up or down, it also gives origin to six of the most important cranial nerves. The origin of these in the medulla, in the various grey nuclei, is an additional complication in the rapidly changing appearance presented by the bulb in successive sections from rear to front. Apart from the complexity of the subject we are now entering on, which increases as we approach the cerebrum, there is also the important fact that in the large herbivora, but with few exceptions, the course of the fibres and the collocation of cells, not only in the bulb, but also in the other centres, are not known with any degree of accuracy.

There is now good reason to hope that the experiments of King* and other observers on the larger herbivora will be the means of laying the foundation of exact physiological knowledge with regard to their nervous system.

The bulb in the horse is wider and more flattened than the cord; it is about 2 inches in length, and is wider anteriorly than posteriorly; it is considered to begin at the first cervical nerve and end at the pons. In this short length of nervous material, functions of vital importance are carried out, through the medium of those cranial nerves which take their origin from this part. On the ventral surface of the medulla two well-marked structures exist, known as the *pyramids*. There is no surface enlargement indicating the presence of the *olivary bodies*, so prominent a feature in man, but in the substance of the medulla well-marked olivary nuclei exist. The pyramids are formed by the collection of motor fibres descending from the brain, and brought together in two bundles in the bulb. In the pyramids they decussate, so that fibres from the right brain pass down the left side of the cord, and *vice versa*. It is more convenient to build up the bulb from below, so that, though the pyramidal fibres are passing out of the brain, they are, from a constructional point of view, spoken of as if they were passing the other way. This being so, it is usual to describe the pyramidal fibres in the cord as crossing in the medulla, and, by so doing, cutting through the ventral horns of the grey matter, and eventually causing these to disappear, as may be seen from sections taken at a higher level. In this way the pyramids are formed, and little is left of the original grey matter. On the dorsal surface of the bulb the two horns open out; the tip of each swells, and forms the *substantia gelatinosa*, while the *columns of Goll* and *Burdach*, which, it will be remembered, have their fibres passing into the brain, end in nuclei known as the *nucleus gracilis* and *nucleus cuneatus* respectively. These are often called the 'leg' nucleus and 'arm' nucleus. The fibres from the above columns terminate by arborising around the cells in their nuclei; those from the anterior half of the body terminate in the *nucleus cuneatus*, while those from the posterior half terminate in the *nucleus gracilis*. From the cells in these nuclei fresh axons are formed, which pass forward into the higher centres, and so still further increase the complex arrangement of the bulb. Incidentally attention may be drawn to the fact that in these nuclei the first sensory spinal neurone, whose seat of origin is in the dorsal root ganglia, has its ending. From these nuclei the second sensory neurone fibres arise, which, passing forwards to the higher centres mentioned above, form the *internal arcuate fibres*. In their journey forwards these decussate above the pyramids, continue their course through the bulb and pons under the name of the *fillet*, and so reach the optic thalamus; here the second neurone ends and the third arises, which passes forwards to end in the post-central gyrus. The *fillet*, or *lemniscus*, is consequently the sensory path connecting the between-brain and the body.

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* *Op. cit.*

The changes made in the arrangement of the medulla having brought the central canal of the cord close to the dorsal surface, it soon opens out into the fourth ventricle; and now a further complexity in the arrangement of the bulb is evident from the fact that the nuclei giving origin to the cranial nerves have here their position, those of the tenth and twelfth pairs being seen forming the grey matter of the floor of the fourth ventricle. The *internal arcuate fibres* cross to the opposite side, enter the *restiform* body which forms the posterior peduncle of the cerebellum, and so gain access to the cerebellum. Some of these arcuate fibres enter the restiform body on its own side. There are also fibres which pass from the *olivary body* through the restiform body of the opposite side to the cerebellum. The *restiform body* is formed in part from the direct cerebellar tract of the cord. The fibres of this tract terminate in the median hemisphere, or *vermis*, of the cerebellum by arborising around the Purkinje cells of that body.

Such, briefly, is the arrangement of the bulb. It is better for the purpose of description to continue carrying the sections forward both through the pons and mid-brain.

The **Pons** lies between the bulb and the cerebral peduncles. If a section be made through it, the appearance presented does not differ materially from that furnished by a section of the upper extremity of the medulla, with the exception that bundles of fibres taking a transverse course are seen passing to the middle peduncles of the cerebellum. Between these fibres is the grey matter, or *nuclei pontis*. From the dorsal surface of the pons are formed the *anterior cerebellar peduncles*. Fibres course through the pons from one side of the cerebellum to the other, and from the cerebrum to the pons. The pyramidal fibres reach into the pons, and are spoken of as the *cortico-pontine*. Though the fibres are described as reaching into the pons from the pyramid, it will be remembered the flow is in the opposite direction, and that these fibres are passing from the cerebral cortex backwards into the cord. In this section can be seen the *nucleus of Deiters*, a collection of large multipolar cells, in the floor of the fourth ventricle, which is intimately connected with afferent and efferent mechanisms, and is one of the cell-terminations of the vestibular branch of the eighth nerve. From this nucleus arises the vestibulo-spinal tract (see p. 500). From the pons arises the important fifth pair of cranial nerves.

A section through the **Mid-Brain** shows that the reticular structure of the pons is continued forward; it is enlarged by fibres derived from the opposite cerebellar cortex, and fibres from the nuclei of the fifth and eighth cranial nerves. The nervous mass formed by these structures bifurcates into the *crura cerebri*, or *cerebral peduncles*, and these constitute the ventral portion of the mid-brain. Each peduncle is divided by a groove into two portions—a dorsal, known as the *tegmentum*, and a ventral, or *crusta*. Between the two is a collection of grey matter known as the *substantia nigra*. In the crusta the motor, and in the tegmentum the sensory fibres are contained; the mid-brain therefore constitutes an important highway between the cerebrum and the body.

Functions of the Bulb.—We have seen that this is the path by which the brain communicates with the periphery and the periphery with the brain. It gives origin to, or is connected with, all the cranial nerves but those of smell, vision, and of the muscles of the eyeball. It is the supreme reflex centre for all the mechanisms of the body most important to life, such as respiration (p. 137), circulation (p. 87), the action of the heart (pp. 58-60), and of the digestive apparatus from the pharynx to the large intestine (pp. 165, 197, 217, 234). It is astonishing that these varied functions can be discharged by a few inches of nervous tissue. If the medulla be cut off from the brain in front of its various centres, the animal continues to live, respirations are regulated, the blood-pressure is maintained, and the heart continues under control. If the section be made behind the centres, all is at once changed, because the respirations cease instantaneously; the blood-pressure sinks dangerously, but then partially recovers, rising in the cat and dog to a height of about 90 mm. (instead of the normal 130). The heart beats slowly but well, and the animal dies from asphyxia (see p. 138). If artificial respiration be established, the beat of the heart may be maintained for some days. The animal is conscious, feels pain if the lip be pinched, blinks when the finger approaches the eye, feels hunger, and will even seize food within its reach, masticate and swallow it (Chauveau).

The centres located in the bulb are those for mastication, swallowing, sucking, vomiting, respiration, phonation, coughing, the regulation of the heart-beat and arterial calibre, movements of the iris, the secretion of saliva, the glycosuria centre, and a centre for the sweat glands. The bulb and pons contain centres which are intimately associated, through centres in the spinal cord, with the reflex act of standing.

The **Mid-Brain** is composed of the *corpora quadrigemina* and *cerebral peduncles ;* these form the basal ganglia.

The Corpora Quadrigemina.—The white matter of the anterior of these bodies is derived from the optic nerve, the fibres of which arborise around its cells. Fibres from the corpora quadrigemina also run backwards to the cord, and in man gain a tract known as the infero-lateral descending. The anterior pair of bodies is concerned in vision. It forms a reflex arc connected with the movements of the pupil, while, through its connection with the optic nerve, it works upon the muscles of the eyeball. The posterior corpora quadrigemina are important in the higher group of vertebrates—viz., birds and mammals which have a cochlea—that is, a 'hearing' ear, besides an 'equilibrating' ear. They receive fibres from the cochlear nerve, and have reflex centres concerned with the lower auditory functions and with vocalisation.

The Optic Thalamus.—As we have previously seen (p. 504), this is the junction for all afferent impressions prior to distribution to their destination. It is especially the main sensory station, the seat not only of painful, but also of pleasurable impressions. Its activities, especially in the higher animal, are controlled by the cerebral cortex, and failure to exercise the necessary control was the explanation of the neurotic condition produced in many during the Great War. It may be argued that among the lower animals cerebral control over the emotional thalamus is difficult to prove, while it is easy to show how frequently it is never exercised. Most animals respond to painful impressions and endeavour to escape from them; the painful impression may be either physical or moral. The horse of all others is susceptible of panic, and in these cases there is an inability on the part of the cortex to control the thalamus. On the other hand, a dog while fighting will submit to severely painful impressions without relaxing its hold, and a 'jibber' may be utterly indifferent to whip or spur. In such cases the thalamus is controlled.

Head,* however, points out that the normal control of the cortex is an automatic and not a voluntary act, and that the moment it becomes voluntary a conflict ensues which leads to a break-down. It is difficult to determine the extent to which this holds good in animals. Horses when first taken into military training meet with sights which to them are terrifying, but confidence is soon established. We never remember an animal having to be rejected from the service owing to a failure to overcome its natural nervousness during training, though the flutter of a lance flag or wave of a sword frequently create more apprehension than the discharge of a rifle. The artillery horse who does not blink an eyelid at the noise made by his own guns dislikes the crackle of rifle-fire when he first hears it, and the cavalry horse who is indifferent to rifle-fire may be felt suddenly to 'open out' and contract under the rider when he first meets with artillery fire. In all cases the control exercised by the cortex must at first be voluntary; later, it is of course automatic. On the other hand, the elephant, in spite of his intelligence, can never be trusted under fire.

The structure of the thalamus suggests that it is also connected with motor functions, for destruction of portions of the cortical area leads to degeneration of their corresponding nuclei in the optic thalamus. Connected with the thalamus is the *red nucleus*, which gives origin to an important spinal motor path in the lower animals (see p. 500). Some observers have considered that secretory, vasomotor, and other fibres connected with the sympathetic system, are represented in the thalamus. Cauterisation of the thalamus in pigeons has recently been stated to render the animal permanently cold-blooded (F. T. Rogers), so that it would appear in some way to be associated with the regulation of body temperature.

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* 'Elements of the Psycho-Neuroses,' *British Medical Journal*, March 20, 1920.

The Corpus Striatum.—Lesions of this body are said to be associated with a rise in temperature; hence it has been looked upon as governing heat production. Little is known of the subject, but it is supposed that impulses pass to the skeletal muscles, causing an increased production of heat. Developmentally the corpus striatum is a part of the cerebral cortex, and not a portion of the old mid-brain. The corpus striatum is interesting clinically on account of the comparative frequency with which it is diseased in the horse. There are no symptoms pointing to cerebral trouble until a day or two before death. It is remarkable to what size a growth in this body may attain before any symptoms of pressure are shown. These cases should enable the question to be settled of the connection, if any, between the corpus striatum and body temperature.

Experimental injury of the corpus striatum of the horse was carried out by Colin, who found that a simple puncture caused no inconvenience or interference with locomotion. Three fresh punctures made in the same corpus produced immediate paralysis of the hind-legs, and the animal could only be kept standing by a support under the belly. When walked thus supported, the fore-limbs were quite unaffected, the hind-limbs dragged. If the animal fell, power appeared to be regained in the hind-legs, for he was able to recover the standing position. The paralysis gradually passed away, and the horse was able to stand without assistance.

SECTION 5.

The Cerebellum.

The cerebellum is broadly divided into a central body, known as the *vermis*, or worm, and two hemispheres which lie on either side of the central body. It is situated above and in front of the medulla, and is remarkable for the curious foldings of its grey and white matter, which give it a characteristic appearance on section. The grey matter is placed externally, a reversal of the order found in the cord. The *grey matter* of the cerebellum is found to consist microscopically of two layers, an outer and inner. In the *outer or molecular layer* two types of cells are found: one is known as a 'basket cell,' from the peculiar manner in which its axon dips down and encloses the large characteristic cells of Purkinje, which are placed between the outer and inner layers of the cortex (Fig. 148). In the second type of cell found in the outer layer of the cortex the axons run longitudinally to the surface of the cerebellum, giving off collaterals which dip down and arborise around the dendrites of the cells of Purkinje. In the *inner or granular layer* of the cortex the cells are small, their axons travel towards the surface of the cerebellum, where a **T**-piece is formed, which, running parallel to the surface, makes connections with the dendrites of the Purkinje and other cells, such as those of Golgi's second type, which are also present. Purkinje's cells, as above mentioned, are placed between the two layers of the cortex. They are distinguished by their considerable size and by possessing a single dendrite, which breaks up into a remarkable branching tuft and runs towards the surface of the organ, while the axon passes into the white matter, giving off collaterals (Figs. 149 and 150).

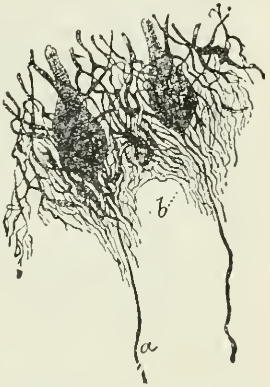

FIG. 148. — PERICELLULAR BASKETS (SCHÄFER, AFTER RAMON Y CAJAL).

Two cells of Purkinje from the cerebellum are seen surrounded by end ramifications forming a basket-work: *b*, derived from the branching of axons; *a*, of small nerve-cells in the molecular layer.

The *white substance* of the cerebellum consists of both afferent and efferent fibres; the afferent fibres—viz., fibres afferent for the cerebellum—are found microscopically to consist of two varieties, which, from peculiarities in their arrangement and distribution, are known as '*moss*' and '*tendril*' fibres. The 'moss' fibres terminate by branching in the nuclear layer of the grey matter, while the 'tendril' fibres pass into the molecular layer, and arborise by climbing around the dendrites of the cells of Purkinje. The efferent fibres are the axons of the cells of Purkinje, which are essentially efferent in function. The above outline affords some notion of the complexity of the structure of the cerebellum; it is anticipating matters to say that this body is the centre of an important reflex arc, but it is evident from its structure how well it is arranged for reflex processes.

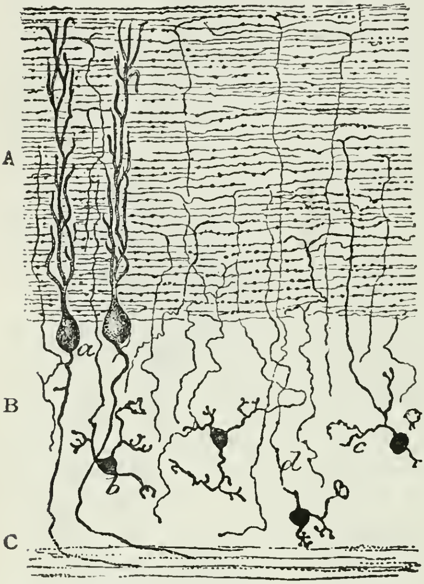

FIG. 149.—CEREBELLAR CORTEX: SECTION IN DIRECTION OF LAMINA (CAJAL).

A, Outer or molecular layer; B, inner, nuclear, or granular layer; C, white matter. *a*, Purkinje's cell; *b*, granule cells of inner layer; *c*, dendrite of a granule cell; *d*, axon of a granule cell passing into the molecular layer, where it bifurcates into two fine longitudinal branches (Golgi's method).

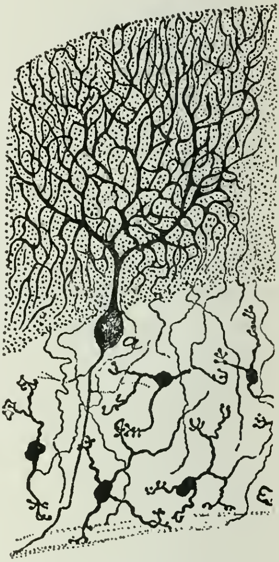

FIG. 150.—CEREBELLAR CORTEX: SECTION ACROSS A LAMINA (CAJAL).

a, Purkinje's cell; the numerous dots in the molecular layer represent cross-sections of the bifurcated axons of the granule cells (Golgi's method).

The cerebellum, by means of its three peduncles, is brought into connection directly or indirectly with all the other parts of the brain. The incoming fibres sweep through the peduncles and terminate in the grey matter in the manner already described. The efferent fibres originating in the cells of Purkinje do not pass out through the peduncles directly as fibres derived from the cortex; these cortical fibres first terminate in nuclei, and from the cells of the nuclei fresh fibres are formed.

Through the *anterior peduncle* fibres pass from the cells of Purkinje to the mid-brain. This is the only purely efferent tract assigned to the cerebellum, and the distribution of the fibres is peculiar and complex. The peduncles converge and meet in the mid-brain; by their so doing their fibres decussate, so that impulses from the cerebellum pass to the opposite side of the brain, where they are conveyed to the red nucleus. This is the second cell station for the efferent fibres. In the red nucleus, some of the fibres are sent upwards to the cerebral cortex by means or fibres known as *thalamo-cortical,* and others pass backwards by a special tract known as the *bundle of Monakow,* or *rubro-spinal tract,* which in its passage to the medulla crosses the central line, so that impulses pass down the lateral columns of the cord on the same side as they issue from the cerebellum. In this way the cerebellum is brought into communication with its own side of the cord, an arrangement which is in contrast to the connection existing between the cerebrum and spinal cord, which is crossed. By means of the anterior peduncle the fibres of the *ventro-lateral ascending tract* of the cord (tract of Gowers) also gain entrance to the cerebellum, being distributed to the lower part of the *vermis.*

By means of the *middle peduncle* the cerebellum is brought into communication with the *pons,* fibres passing from nuclei in the pons to the cerebellum. This is the second indirect path between the cerebrum and cerebellum, but in this case it is afferent—viz., the communication is from cerebrum to cerebellum.

Through the *posterior peduncle,* which is formed by the restiform body of the medulla, runs another important afferent path to the cerebellum, but in this case from the spinal cord. The direct cerebellar tract passes unbroken through the bulb, through the posterior peduncle, its fibres being mainly distributed to the *vermis* on the same side. Other very important fibres constituting a connection between the cerebellum and the labyrinth are conveyed by this peduncle from the eighth pair of cranial nerves. The eighth pair of nerves arises from two roots; one from the vestibule of the ear is in no way connected with the sense of hearing, but is entirely devoted to the question of body equilibrium and allied matters. This branch gains access to the cerebellum through the posterior peduncle. It will be observed that the posterior peduncle is a second afferent path to the cerebellum.

The cerebellum is connected, as we have now seen, with the mid-brain, cerebrum, medulla, and spinal cord. It is doubtful whether its two halves are connected. Afferent impulses may pass to the cerebrum via the cerebellum, and efferent impulses from the cerebrum to the muscles may reach them through the cerebellum. Afferent impulses may pass to the cerebellum and efferent impulses issue from it without the intervention of the cerebrum.

Functions of the Cerebellum.—Our knowledge respecting the uses of this organ is still very incomplete. Flourens regarded it as being connected with locomotion and the problem of body-balance. The study of comparative anatomy lent support to this theory; it was observed how highly the cerebellum was developed in birds and in swift-swimming fishes with great locomotive power, such as the shark. In birds the *vermis* of the cerebellum is large and deeply folded, though the hemispheres are almost wholly absent, excepting in those birds which remain some time in the air and possess wings and feet of considerable strength. The experiment of Flourens on the cerebellum consisted in its removal in the pigeon; as the result of the operation the bird was unable to fly, stand, or feed itself. When it attempted to walk, spasm of the extensor muscles of the legs occurred, and it fell, struggling wildly, in a state of evident panic. There was no muscular paralysis, but the pose of the body was awkward, the head being drawn back and neck twisted. During the muscular spasms the contractions led to the animal turning somersaults. In course of time the violent symptoms disappeared, and the bird was able to fly, but for a long time was unable to perch, through spasms of the extensor muscles of the limbs. When the cerebellum is sliced away, and not entirely removed, the gait is rendered uncertain and staggering, and there is inability to maintain equilibrium.

In the dog injury to one hemisphere of the cerebellum leads to the animal moving in a circle or rolling towards the injured side, and to a disturbance of co-ordination. The entire cerebellum, however, has been removed in the dog, and the animal remained alive for many months. In these cases there are muscular spasms of the head, neck, and fore-legs, weakness of the hind-limbs, and when the eyes are closed standing is impossible. When the acute symptoms pass away the animal is left with a deficiency of muscular tone. It is interesting to note that this lesion does not prevent the dog from swimming.

Colin exposed the cerebellum in a draught horse, and punctured the middle lobe, or *vermis*, with a scalpel. The animal at once shook his head, but there were no convulsions. After a second and third puncture the gait became staggering and the limbs splayed to preserve the equilibrium. When the animal walked, the body was balanced alternately to the right and left, as if at each step he expected to fall. In the walk he showed a marked tendency to lean forward in the attitude of draught, as if determined to negotiate a stiff hill; it was only with difficulty that seven or eight assistants held him back.

The cerebellum has been regarded as the centre of muscle sense—*i.e.*, as the centre by which the position of the body and its movements are recognised in the absence of visual and tactual impressions. The necessary impulses are brought to it from the foot-pads in soft-footed animals, also from the depths of the body—*i.e.*, the muscles, tendons, ligaments, joints (pp. 491, 504)—and, as we shall presently see, from the internal ear. Loss of sensation in the soles of the feet in man leads to disturbances of equilibrium; in animals this does not appear to be so. A cat may have its feet desensitised by division of all sensory nerves with no evident interference with locomotion, and in the solid-footed horse robbing the part of sensation gives similar results.

The importance of maintaining the body equilibrium, a power markedly lost as the result of injury or disease of the cerebellum (cerebellar ataxia), is explained by the connection which exists between the cerebellum and the internal ear. This connection is the most important path by which afferent impressions associated with the mechanism of equilibration are conveyed. The nerve from the semicircular canals enters the pons and connects with the nucleus of Deiters, which in turn connects with the cerebellum. Through the nucleus of Deiters the vestibular nerve is brought into indirect communication with a nucleus which gives rise to the nerves supplying the muscles of the eyeball, and by means of the vestibulo-spinal tract (see p. 500) it establishes connection with the motor cells in the spinal cord. The influence of the semicircular canals on equilibration will receive consideration in treating of the organs of special sense; briefly it is due to afferent impressions received by the cerebellum from the semicircular canals that the cerebellum is enabled to judge of the position of the body in space. The receptors of the labyrinth and the deep receptors of joints and muscles are stimulated by the animal itself, such as by movements of the joints, while the surface receptors (*extero-ceptors*) are stimulated from without. The deep receptors (*proprio-ceptors*) of a limb can, however, influence only the tonicity of the muscles of that limb, while those of the labyrinth influence not only the limbs and the trunk, but the head and muscles of the eyeball. In consequence the limb influences are mainly concerned with the relation of the limbs to other portions of the trunk, while the influences from the labyrinth regulate the position of the body generally towards the external world and the anti-gravitational reflex of standing (Sherrington).

The maintenance of equilibrium and the sense of direction are associated with movements of the eye muscles, the labyrinth furnishing the necessary information as to the relationship of the body to surrounding objects. One of the earliest indications of disease of the spinal cord may be an inability to walk in the dark, and we have seen that a dog without a cerebellum cannot move with the eyes covered. The cerebellum is furnished with the needful information through its indirect connection with the third and fourth pairs of cranial nerves, which govern the movements of the eyeball. It would appear that the biped derives more information from perceiving the position of the limbs relatively to the body than is afforded the quadruped, whose eyes are in advance of the limbs. The writer has never known a horse refuse to advance, even on the darkest night, provided the ground be good. If it is broken, he travels with care; if boggy, he may refuse to advance. Without seeing his limbs or surrounding objects, he moves over unbroken ground as safely in the dark as in the light, while his sense of direction over ground he has previously travelled is so excellent that the man who has lost his way may safely leave the solution of the problem to his horse.

Each half of the cerebellum controls the muscular system on its own side of the body, and each half receives impulses from the opposite cerebrum. It appears likely that definite regions of the cerebellum govern definite body areas. It can be shown experimentally that a particular region of the cerebellar cortex controls movements of the fore-limb, another governs a hind-limb; others cause rolling or bending movements of the body, or conjugate movements of the eyes. The posterior portion of the *vermis* is concerned mainly in muscular co-ordination, and in some of the lower animals is the only portion of the cerebellum represented.

SECTION 6.

The Cerebrum.

The cerebrum is composed of grey and white matter, the grey being externally placed like a mantle and thrown into convolutions. The use of the convolutions is to increase the area of the grey matter, and their depth has been supposed to bear some relationship to the intelligence of the animal. There are many animals whose cerebra are quite smooth; there are others, like the bear, seal, and whale, whose cerebra are much more convoluted than in man.

Weight of brain in relation to body weight has been suggested as a measure of intelligence, and when the comparison is made among animals of the same group it may be possible that the heavier brains are the more intelligent. Weight of brain may, however, depend upon such factors as fluid, white matter, and grey substance. Colin compiled an elaborate series ot tables of weight of the cerebral nervous system in animals, and showed that the proportion of brain to body weight was as follows:

Man - - - - - - -	1 to 52
Cat - - - - - - - -	1 ,, 99
Dog - - - - - - - -	1 ,, 235
Rabbit - - - - - - -	1 ,, 295
Sheep - - - - - - -	1 ,, 317
Ass - - - - - - - -	1 ,, 332
Pig - - - - - - - -	1 ,, 369
Horse - - - - - - -	1 ,, 593
Ox - - - - - - - -	1 ,, 682

For every kilogramme of body weight—

Man requires - - - -	19·00 grammes of brain.
Cat requires - - - -	11·37 ,, ,,
Dog requires - - - -	4·80 ,, ,,
Rabbit requires - - -	3·31 ,, ,,
Sheep requires - - -	3·00 ,, ,,
Ass requires - - - -	2·46 ,, ,,
Pig requires - - - -	1·90 ,, ,,
Horse requires - - -	1·68 ,, ,,
Ox requires - - - -	1·47 ,, ,,

In proportion to its size, a mouse has more brain than a man, thirteen times more than a horse, and eleven times more than an elephant; a cat has much more than a dog; a rabbit nearly approaches a dog. It is evident that outside the animal group the relative weight of brain to body is of limited value as a standard of intelligence. The modern method of determining the mind of an animal from the structure of the cortex of the cerebrum will be dealt with later on.

Structure of the Cortex.—The cerebral cortex is made up of several layers of cells, the number of which is not agreed upon by histologists, but it may be regarded as consisting of four principal layers. These layers vary in different animals, and we are compelled, as in other portions of the physiology of the nervous system, to fall back upon what is known of the subject in the dog, pig, and man, in the absence of direct information regarding the horse. The layer of cells immediately beneath the pia mater is spoken of as the *molecular ;* it consists of some very small nerve-cells with their dendrites and axons, also of dendrites projecting from cells deeper seated in other layers, and the terminal processes of axons belonging to fibres coming from other regions. Perhaps the distinct feature of the layer is the structure first spoken of, the small cells with their dendrites and axons. These begin and end in this layer, and appear to be of a linking-up, or, as it will be described later, associative nature. In the second layer are *small pyramidal cells,* with the apex towards the surface and the axon passing inwards to the white substance. The depth of this layer increases the higher the animal scale is ascended. Next comes a layer of *large pyramidal cells,* sometimes called ‘ giant pyramids of Betz,’ found mainly in that portion of the brain anterior to the fissure of Rolando,* and in particular in the region of that fissure. These cells are of great physiological importance, as from them the fibres constituting the great motor tracts are derived. The last layer is that of *polymorphous cells,* which are, generally speaking, small, and many of them fusiform in shape. With these are cells of Golgi of the second type; but whereas the axons of the former pass inwards to form white fibres in the medullary portion, the axons of the Golgi cells pass outwards and end by arborising in the molecular layer. The functions of the cerebral cortex have been examined, not only by the method of direct experimental excitation, but also from the histological side; this has enabled the cortex to be mapped out into different regions, and in this connection it is desirable to make clear that the histological method does not wholly consist in comparing the structure of one fully-developed area with another, but also in studying the periods at which the fibres leading to the area assumed their sheath of myelin, both in the embryo and young animal. This line of research is especially associated with the name of Flechsig. The study of the structural features of the brains of imbeciles and of other pathological conditions has also largely contributed to a more exact knowledge of the uses of the various parts of the cortex.

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* It is convenient for the present to retain the term ‘ fissure of Rolando ’; it will be pointed out later that there is no fissure of Rolando in the dog, nor is the *crucial fissure* of this animal, in the vicinity of which the motor area is located, the equivalent of the fissure of Rolando.

The structure of the cortex points to its being a collection of reflex arcs, the complexity of which differs according to the animal scale. The cortices of man and of the frog possess the same anatomical elements, but the complexity of the neurones of the former are in marked contrast to the simplicity which distinguishes those of the frog (see Fig. 151). A rich system of dendrites means more numerous and complex connections, and evidence has recently been brought forward to show that there are structural peculiarities accompanying specialisation in function, to which attention will be drawn later.

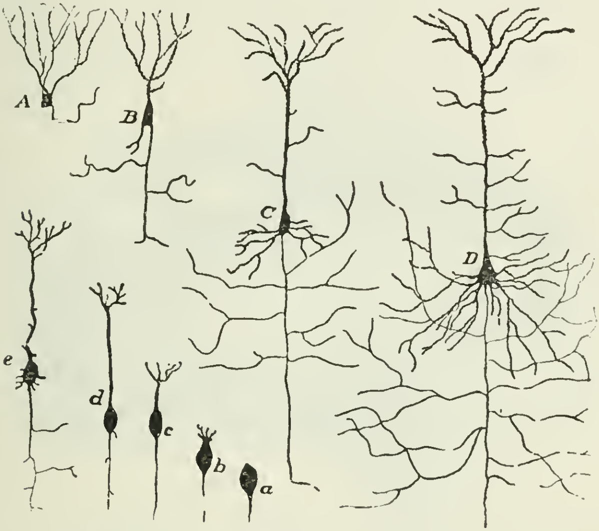

FIG. 151.—PYRAMIDAL CELLS OF CEREBRAL CORTEX IN DIFFERENT ANIMALS (DONALDSON, AFTER RAMON Y CAJAL).

A—D shows the several degrees of complexity in the fully developed pyramidal cells in different vertebrates: A, frog; B, lizard; C, rat; D, man. *a*—*e* shows the development of the pyramidal nerve-cells of the cerebral cortex in a typical mammal: *a*, neuroblast with commencing axon; *b*, dendrites appearing; *d*, commencing collaterals.

In the *white substance* of the cerebrum are nerve-fibres conveying impulses to the cortex, either from different parts of itself or from the basal ganglia, bulb, and cord. There are also present efferent fibres which have their origin in the cells of the cortex, and which pass to different parts of the brain, or out of the brain via the bulb and cord. Fibres which pass from one part of the cortical convolutions to another belong to the linking or *association* system (Fig. 152). Fibres which pass to the opposite side of the brain via the corpus callosum belong to the *commissural* system, while the masses sweeping out from the cortex and connecting it with the mid-brain, pons, bulb, and spinal cord, belong to the *projection* system. In Fig. 153 the projection system in the human brain is shown. It is not wholly efferent—that is to say, it does not consist entirely of motor fibres passing out to the pons, bulb, and spinal cord. The motor tracts form only a part of the projection system, which in addition contains sensory, visual, and auditory tracts, and fibres travelling from the frontal lobes to the cerebellum.

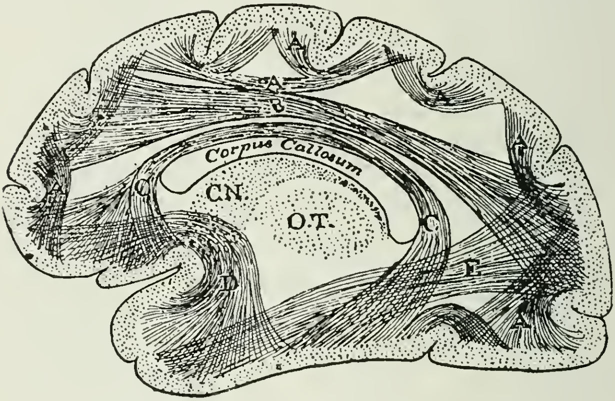

FIG. 152.—ASSOCIATION FIBRES (AFTER STARR).

Human cerebral hemisphere seen from the side. A, A, Association fibres between adjacent convolutions; B, between frontal and occipital lobes; C, cingulum connecting frontal and temporo-sphenoidal lobes; D, uncinate fasciculus between frontal and temporal regions; E inferior longitudinal bundle between occipital and temporo-sphenoidal lobes; O.T., optic thalamus; C.N., caudate nucleus.

The **Great Efferent or Motor Path** in man is formed, as we have just seen, from the large pyramidal cells in the cortical layer of that portion of the cerebrum anterior to and bordering on the fissure of Rolando, precentral gyrus, and travels backwards and downwards through the corona radiata, internal capsule, and peduncles of the cerebrum to the pons (Fig. 153), B. From this large tract are detached the motor fibres connected with the cranial nerves, and these cross to the opposite side of the brain. The larger mass sweeps onwards through the bulb, and there in the pyramids the system decussates, the fibres crossing to the opposite side of the cord. In the cord, cell connections are formed all the way along, either by means of collaterals or by the fibres actually terminating; in either case synapses are formed around the cells in the ventral horns of grey matter. From these axons arise which eventually form the motor roots of the spinal nerves. From the motor roots the fibres pass to the muscles, where they terminate in *end-plates*. It will be observed that there are two neurone systems in this path, one between the cortex and the cord (pons for the facial muscles), the other between the cord and the muscle. From the moment these fibres start on their journey from the cortex connections are constantly being formed with neighbouring structures by means of synapses, not only in the cortex, but in the mid-brain, pons, bulb, and, as we have seen above, in the cord. It has even been considered that in their passage along the cord the two tracts exchange

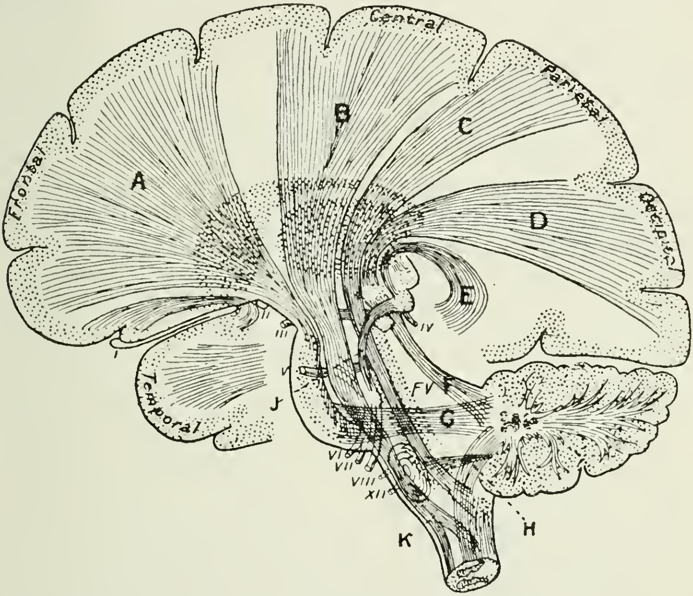

FIG. 153.—PATHS FROM CORTEX IN CORONA RADIATA, HUMAN (STARR).

A, Tract from frontal convolutions to nuclei of pons and so to cerebellum; B, motor pyramidal tract; C, afferent tract for tactile sensations (represented in the diagram as separated from B by an interval for the sake of clearness); D, visual tract; E, auditory tract; F, G, H, superior, middle, and inferior cerebellar peduncles; J, fibres from the auditory nucleus to the posterior corpus quadrigeminum; K, decussation of the pyramids in the bulb; FV, fourth ventricle. The Roman numerals indicate the cranial nerves.

fibres. In this way is formed the tract for voluntary body movement which we have studied at p. 499 under the name of the 'crossed pyramidal tract.' It is the path by which movements of which the animal is distinctly conscious are effected. The brain starts or instructs the movement, the mechanisms in the cord carry it out. The apparently purposeful muscular movements initiated by the cord of the animal immediately after death warrants the supposition that quadrupeds are in much the same position as the decerebrated frog. The limbs are represented in the cortical area of the fissure of Rolando, and they are also represented in the grey matter of the spinal cord, the great difference between the two centres being that one is exercised voluntarily, while the other is involuntary, until the moment arrives when the pulling of the needful switch brings it under the control of the higher centres.

We shall see presently that the entire cerebral cortex may be removed from the frog, pigeon, and dog, and the motor area from the sheep, without producing in these mammals more than a marked loss of power, which is regained in time. In such cases the centres in the cerebrum controlling the muscles are entirely cut off from them, and other motor tracts have to be found. In the dog it is suggested that the rubro-spinal tract (p. 500) fulfils this function. In the sheep we have seen (p. 500) that motor fibres are only in part derived from the cerebral cortex, and that a subcortical supply is furnished by the mid-brain, pons, and medulla. There can be little doubt that a similar arrangement exists in the other herbivora.

The neurone relay between cortex and end-plate is the explanation of a peculiarity observed in muscular paralysis in man. When the neurone between the cord and the muscle is affected, the paralysis is complete; but when the pyramidal neurones—*i.e.*, those between the cortex and the grey matter of the cord—are alone affected, there is a path left open for reflex stimulation, and those impulses normally passing to muscles from the cerebellum, which have been spoken of as 'tonic,' throw the paralysed limbs into a condition of continuous contraction. This is spoken of as *spastic paralysis*.

The **Great Afferent or Sensory Path** conveys impulses evoking sensations—heat, cold, touch, and pain—also such senses as are not normally recognised—viz., muscle sense, joint, tendon, and viscera sense, and the senses of vision, hearing, smell, and taste. This path is broken by at least three sets of synapses: (1) in the cord; (2) in optic thalamus; and (3) in cortex cerebri. The optic thalamus is practically the meeting-place or junction of the whole afferent system on its way to the cerebral cortex (Fig. 147).

Impulses conveyed by sensory nerves pass through the spinal ganglia, enter the spinal cord, and reach the medulla by the dorsal columns of the cord. In the dorsal columns of the cord they travel on the side on which they enter, and finally reach the medulla in the gracilis and cuneate nuclei, where they arborise. Through the fresh fibres arising from the nerve-cells of these nuclei the impulses cross to the other side of the medulla, and by means of the *fillet* reach the mid-brain and optic thalamus. From the thalamus the fibres of the third sensory neurone are distributed by means of the internal capsule to that portion of the cerebral cortex lying behind the fissure of Rolando—viz., the post-central gyrus. Impulses which, though afferent, are probably not sensory, but for reflex work, gain the medulla via Clarke's column. The spinal roots on entering the cord arborise around the cells in this column, and by means of the fibres forming the dorsal and ventral cerebellar tract they reach the brain as follows: The dorsal (direct) cerebellar tract passes by means of the restiform body into the superior part of the *vermis*, while the ventral cerebellar tract runs along the lateral columns to the pons, passes beneath the roots of the fifth nerve, and then bends back to end in the superior vermis of the cerebellum. It is by means of the lateral columns that pain-provoking impressions are conveyed from both halves of the body. These impulses having reached the pons, pass to the optic thalamus, which is the sensory relay station to the cortex and the seat of pain.

The **Association System** of fibres is employed in bringing the various parts of the brain into connection—convolution with convolution, lobe with lobe, cerebrum with mid-brain, cerebellum, and pons. Some fibres, the **commissural**, connect the right side with the left in all its anatomical parts, the *corpus callosum* being the largest member of this system. The system of association fibres links up the various parts of the brain and affords routes innumerable for the passage of impulses to and fro. It has been previously mentioned that the complexity of the dendrites of the cells bears some relation to the scale of brain development in the animal kingdom; it may now be noted that the more profusely branched the dendrites the larger the number of paths there are in the association system.

Functions of the Cerebrum.

The cerebrum is without sensation; it can be handled, cut, or otherwise injured without any sign of pain being elicited. For many years it was considered, in consequence of the experiments of Flourens, that the cerebrum was a homogeneous organ, and all of its parts functionally of the same character. It was known to be connected with the higher faculty of intelligence, but that it was an organ containing within itself other organs functionally distinct, yet intimately connected, was never anticipated.

We have seen that the decerebrated frog is a reflex machine, but from animals so low in the scale it is difficult to obtain any real knowledge of the function of the organ.

Removal of the Cerebrum.—The pigeon with the cerebrum removed becomes converted into a drowsy, lethargic animal, unable to feed itself, though it may try in an aimless manner to do so. It can fly and perch, may be awakened by a loud noise, shows no fear, and is not possessed of maternal feeling. It may awake sufficiently to preen itself and gape, and then once more returns to its condition of somnolence. So far as can be judged, the chief loss this animal has experienced is that of memory.

Colin removed the cerebrum in horses. He notes that the animal fell almost before the superficial layer had been taken away. A horse so dealt with was unaffected by stimulation, gave no indication of feeling pain, noises were not heard, light had no effect upon the pupil, and there was no eyelid reflex. Ammonia applied to the nostrils caused no irritation, and taste and all special senses were lost. In the case of the decerebrated heifer the animal was able to stand, but could not see; hay was held in the mouth and not masticated,* and no notice was taken of the blowing of a horn.

If partial destruction of one hemisphere in the horse be practised, the animal may be kept on its legs for a short time. The superficial layer of the right cerebral lobe was removed in the ass, and the animal remained standing for nearly an hour. The limbs on that side were slightly bent under the influence of the body weight, and the animal moved with difficulty, and, if left to himself, remained immobile. When made to walk he walked very quickly, now and then in a circle in the direction opposite to the lesion. If he walked into anything he fell, but could be raised. In another ass the left hemisphere was incised in the direction of its length, and immediately hemiplegia occurred on the right side; the animal fell on that side, and could not be got up again. In many horses a puncture through the entire thickness of the cerebral lobes sometimes sufficed to cause the animal to fall and to be unable to rise. Bovines withstood far better than equines mutilation of the cerebral lobes. A heifer with one cerebral lobe removed remained standing for more than half an hour, retained its vivacity, and walked with such ease that it was extremely difficult to observe the muscular deficiency

* A common symptom in the horse suffering from brain trouble.

on the side opposite to the lesion. When the remaining lobe was removed, she could still stand up, but could move only forwards, backwards, and turn with great difficulty.

Injury to one cerebral peduncle in the rabbit was found by Longet to lead to ménage movements towards the opposite side; but if the peduncle were cut through, the movements did not occur. Colin found that ménage movements were performed by the horse when a cerebral peduncle was injured. He pricked the left peduncle, and observed that the head was at once carried to the right, and the neck and body bent, so that the muzzle became applied to the flank, and sometimes to the thigh, as if the animal were bent in halves; the limbs were gathered in a bunch under the body, and the animal rotated on a small pivot. When turning, it frequently fell, but the body still remained curved; when raised, the circular movements were repeated. The horse could go backwards, but could neither advance nor turn to the left.

Colin destroyed the corpus callosum, and observed that he produced neither pain nor convulsions. Longet cut into it throughout its length in young horses and young rabbits, and found there was no sign of pain. The animals remained standing, but could walk or run about if made to. Colin repeated the above experiment on two horses. Both remained standing for a short time; one then fell backwards after some movement of the muscles of the eyeball; the other showed great muscular weakness, and fell on his side. There were no convulsions in either case.

All these observations by Colin were made before anything was known of the function of the cerebrum in connection with skeletal muscles. By his experiments the crossed nature of the pyramidal tract in these animals was clearly proved, and the great independence of the spinal cord in bovines demonstrated.

Goltz removed both cerebral hemispheres by successive stages in a dog, and succeeded in keeping the animal alive for eighteen months. It became a most interesting psychical study. The animal was a mere reflex machine. It could see, but not comprehend; it would show signs of hunger, eat when the nose was brought in contact with the food, but could not recognise food placed near it. After the paralysis succeeding the operation had passed away, the dog could walk slowly and stupidly with its head down. It would growl or bark, turn its head to any spot stimulated, but did not bite. The face was expressionless, and the tail was never wagged. It rejected food of a disagreeable nature, such as meat soaked in a solution of quinine. No matter how hungry it was, this was refused, though the gustatory centres had been removed. The animal slept, but did not dream. She exhibited no sexual excitement or œstrum. Memory, affections, and the capacity to learn were absent; anger was a prominent feature. Goltz's dog exhibited it every day for eighteen months each time she was fed.

One observation in the history of this dog is of extraordinary veterinary interest. The animal in its roaming on one occasion wounded its hind-foot; *it was then observed to walk lame, holding the injured foot off the ground.* It is possible to urge that pain was felt, as some portions ot the brain-stem had been left intact; but Sherrington's remarkable experiment on the decapitated cat disposes of this view.* A cat so treated cannot stand, but it can perform stepping movements with its limbs. 'If, as the preparation lies on its side, one hind-foot be forcibly pinched, this limb is flexed . . . and the other limbs at once begin rapid, co-ordinated stepping movements. The injured foot is held up out of harm's way, and the other legs run away.'†

Removal of an anterior lobe of the cerebrum in the dog leads to unilateral motor and sensory paralysis; the motor paralysis is recovered from, but the loss of muscle sense remains. Removal of the posterior lobes of the cerebrum leads to blindness; there is no paralysis, sensory or motor; the dog remains obedient, but sluggish. Sherrington cut the brain off from the heart and viscera in the dog by division of the cord in the lower cervical region. The animal showed joy, anger, fear, and sorrow. Nothing would induce it to eat dog's flesh, but in this case the olfactory and gustatory paths were still open; in Goltz's dog they had been removed. That 'dog will not eat dog' is a very old maxim, but travellers in the Arctic have recorded the fact that they will do so under stress. Nevertheless, it is remarkable that both the idiot created by Goltz and the dog deprived by Sherrington of all knowledge of its stomach should refuse to eat their own kind. In this matter they exhibit a far nicer discrimination than man.

Observations begun on man in the Franco-German War and continued on animals have demonstrated that the cortex, which it must now be made clear is the elaborating part of the cerebrum—as distinct from the white or connecting matter—contains an area which controls the voluntary muscles of the body, and is known as the **motor area.** Another area connected with body sensibility, such as *muscle sense, touch, pressure,* and *temperature,* is known as the **sensory area,** and comprises not only the body senses above mentioned, but the special senses of *sight, hearing, taste,* and *smell.* The position of these areas is known in the sheep, dog, monkey, and man with considerable accuracy, so that maps of the hemispheres have been drawn up indicating the function of the various localities; the subject is generally spoken of as the *localisation of cerebral function.*

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* *Brain,* part cxxix., vol. xxxiii., 1910.

† These astonishing results show that lameness may be purely reflex in origin. The question of the fitness or unfitness of chronically lame cases to perform work will in time have to be considered afresh. The above observations show with what justice the veterinary profession, as the result of careful observation, has urged in a court of law, though generally without success, that an animal suffering from lameness is not necessarily suffering pain.

The Motor Area.—A region of the brain of the monkey or man, known as the *fissure of Rolando,* is intimately connected with the cells which give rise to the motor nerves passing to muscles. In the dog there is no *fissure of Rolando,* but there is a fissure, known as the *frontal* or *crucial sulcus* (Fig. 154, *c.s.*), in which the motor cells for the muscles are localised as in the fissure of Rolando, and similar localities must exist in other animals, although little has been done to identify them.

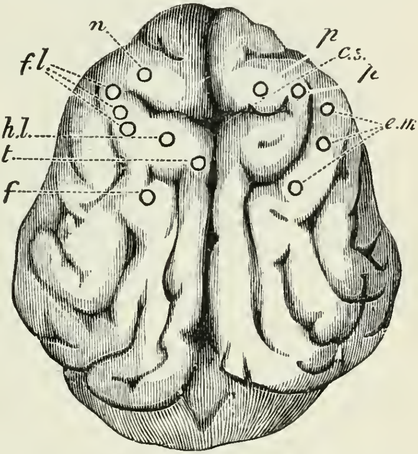

FIG. 154.—MOTOR AREAS OF DOG'S BRAIN (STEWART).

n, Neck; *f.l.*, fore-limb; *h.l.*, hind-limb; *t*, tail; *f*, face (the position here assigned to the facial muscles is unusual; it is generally indicated more laterally and farther forward); *c.s.*, crucial sulcus; *e.m.*, eye movements; *p*, dilatation of the pupil in both eyes, but especially in the opposite eye.

The areas are marked only on the left side of the figure except the eye areas, whose position, to avoid confusion, is indicated on the right hemisphere.

If the brain in the region of the crucial sulcus of the dog be exposed, and the part stimulated electrically, that muscle, or group of muscles, contracts which is connected with those cells of the cortex immediately beneath the electrode. It is remarkable that a great European war was necessary to demonstrate this fact, but physiologists for years remained in this matter under the influence of the teachings of Flourens and Majendie, who stated that the cerebral cortex was inexcitable. Gradually knowledge derived from stimulation of the cortex has accumulated, until a very remarkable picture of the cortical functions can be obtained. Fig. 155 shows the motor area of the chimpanzee; that for man is still more complex. The size of a motor area bears a relation to the degree of complexity of limb movements. The limb movements in quadrupeds are simple; for instance, in the horse they are mainly pendular; in the dog they are more complicated, and still more so in the cat, in which the delicate movements of face-washing are necessarily of a

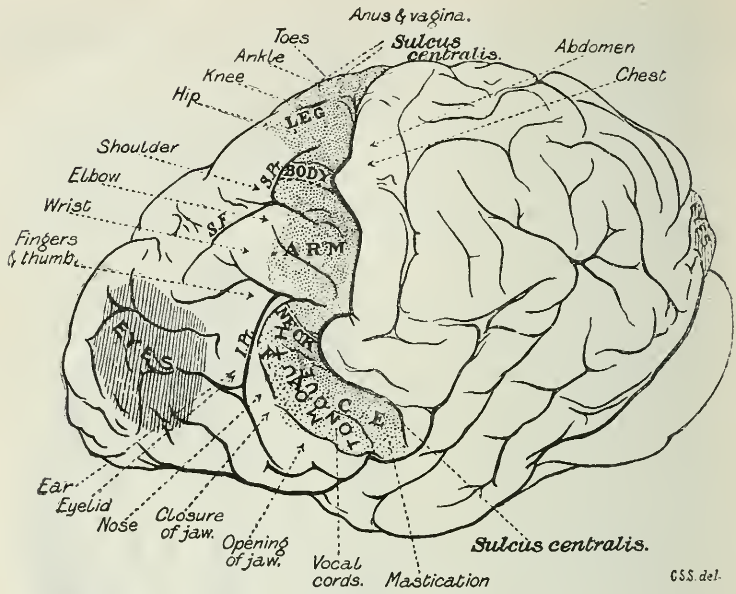
Anus & vagina.
Toes
Ankle
Knee
Hip
Sulcus centralis.
Abdomen
Chest
Shoulder
Elbow
Wrist
Fingers & thumb
LEG
S.P.
BODY
S.F.
ARM
EYES
I.P.
NECK
FACE
TONGUE
Ear
Eyelid
Nose
Closure of jaw.
Opening of jaw.
Vocal cords.
Mastication
Sulcus centralis.
CSS. del.

FIG. 155.—MOTOR AREA OF CORTEX OF CHIMPANZEE (GRÜNBAUM AND SHERRINGTON).

Lateral aspect of the hemisphere.

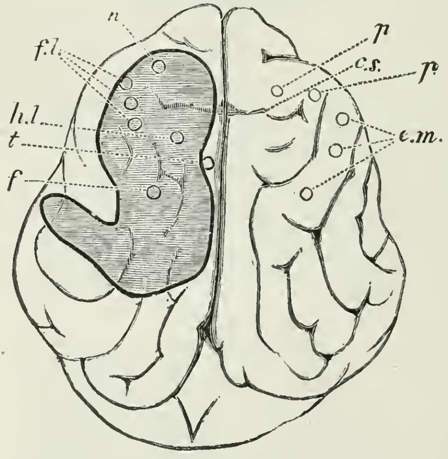
n
f.l.
h.l.
t
f
p
c.s.
p
c.m.

FIG. 156.—DOG'S BRAIN WITH LESION (STEWART).

A portion of the cortex indicated by the shaded area was destroyed by cauterisation. The symptoms were complete blindness of the opposite eye (in this case the right); weakness of the muscles of the limbs and of the neck on the right side; slight weakness of the limbs on the left side. When the animal walked, there was a tendency to turn to the left in a circle. In eating or drinking, the head was turned to the left, so that the mouth was oblique, and the right angle of the mouth was lower than the left. The tail movements were normal, and there was no deviation of the tail to one side.

complex type. In those areas which have been mapped out in the dog, the representation of the muscles of the neck is at *n*, Fig. 154; the fore-limb at *f.l.*; the hind-limb at *h.l.*; face at *f* (see note on Fig. 154); tail at *t*; eye movement at *e.m.*; dilatation of the pupil at *p*. The movements of flexion, extension, and rotation of the various limbs, head, neck, and trunk, and the more complex movements in the higher animals, have each their separate station in the cortex. The more complex and delicate the movements, the larger the cortical representation, so that the head and arm in the ape and man are more largely represented than the trunk and lower limbs, where the movements are of a simpler character. The thumb area is relatively larger than the shoulder or hip area. In Fig. 156 a lesion is shown of the left hemisphere of the dog, involving most of these centres. The symptoms shown are detailed in the description of the figure. In destructive brain lesions it is observed that muscles, like those of inspiration, which act bilaterally, are not affected by a unilateral lesion. We have previously drawn attention to the fact (p. 154) that the muscles of the larynx have a double representation in the cortex—viz., that both sides are represented in each hemisphere, and the same holds good for the respiratory muscles of the chest and abdomen.*

The motor area of the cerebral cortex of one of the larger herbivora has been investigated by Simpson and King.†

These observers have shown that the motor area in the sheep is situated in the superior frontal convolution, and is very limited. This convolution, with the fissures surrounding it, is shown in Fig. 157, while the positions of the motor areas are seen in Fig. 159. The motor area comprises from front to rear centres for (*a*) face, mouth, and tongue; (*b*) head and eyes; (*c*) fore-limb; (*d*) hind-limb. Of these, the fore-limb area is the most, and the face area the least, excitable. The hind and fore limb centres are separated by the *splenial sulcus*; stimulation above the sulcus produces flexion and extension of the opposite hind-limb and spreading of the digits. Flexion is always more evident than extension. Stimulation below the sulcus produces movements of the opposite fore-limb, flexion in this case also being more frequent than extension. Where the fore and hind limb areas meet, and extending from the splenial to the *coronal sulcus* (Fig. 157), is an area common to fore and hind limbs, stimulation of which produces movements of the fore and hind limbs of the opposite side, and sometimes of the hind-limb of the same side, but never of the fore. Stimulation of the head and eyes area leads to turning of the head to the opposite side and conjugate deviation of the eyes. The head movement is deliberately performed as though the animal were turning to look at something behind it.

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* The two-sided representation in each hemisphere is limited to respiration. In other cases each hemisphere causes contraction of chest and abdominal muscles strictly limited to its crossed side, and this is true even of the perineal muscles and *sphincter ani* (Sherrington).

† 'Localisation of the Motor Areas in the Sheep,' Professors Sutherland Simpson and J. L. King, *Quarterly Journal of Experimental Physiology*, vol. iv., No. 1, 1911.

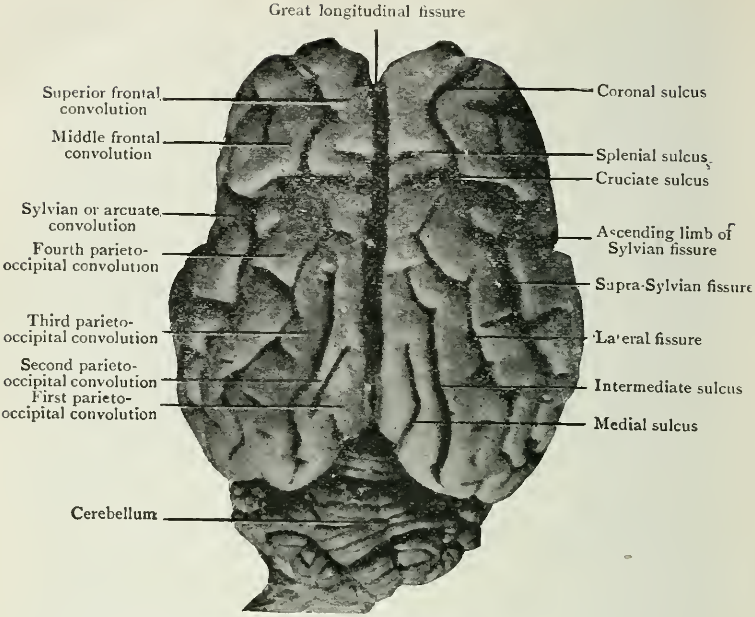
Great longitudinal fissure
Superior frontal convolution
Middle frontal convolution
Sylvian or arcuate convolution
Fourth parieto-occipital convolution
Third parieto-occipital convolution
Second parieto-occipital convolution
First parieto-occipital convolution
Cerebellum
Coronal sulcus
Splenial sulcus
Cruciate sulcus
Ascending limb of Sylvian fissure
Supra-Sylvian fissure
Lateral fissure
Intermediate sulcus
Medial sulcus

FIG. 157.—BRAIN OF SHEEP, DORSAL ASPECT (SIMPSON AND KING).

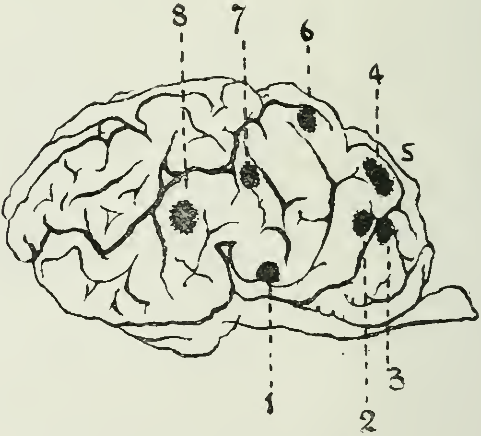

FIG. 158.—CEREBRUM OF HORSE, SHOWING MOTOR AREAS (ARLOING).

1. Movements of limbs; 2, closing movements of jaws; 3, movements of nostrils and upper lip; 4, retraction of the tongue; 5, depression of jaws and flexion of the neck to the opposite side; 6 and 7, blinking and closing of the eyelids; 8, elevation of the upper lid and adduction of the ear.

Below this area is found that for the face, tongue, and lips, which is relatively the least excitable of all, and of which the localisation is the most uncertain. Stimulation produces lip movements, protrusion and retraction of the tongue, but attempts at mastication are rarely made. In lambs this centre is connected with that of sucking, even to the peculiar tail-movements which accompany the act in this animal. No tail-movements can be evoked from this area unaccompanied by sucking.

The exposed cerebrum was found, as in other animals, to be deficient in sensation, painful or otherwise; and extirpation of the motor area led to no limb paralysis. The animal walked as well without the superior frontal and middle frontal convolutions as with them. Further, it was quite unaffected as the result of the experimental procedure, and, when liberated, at once began to eat.

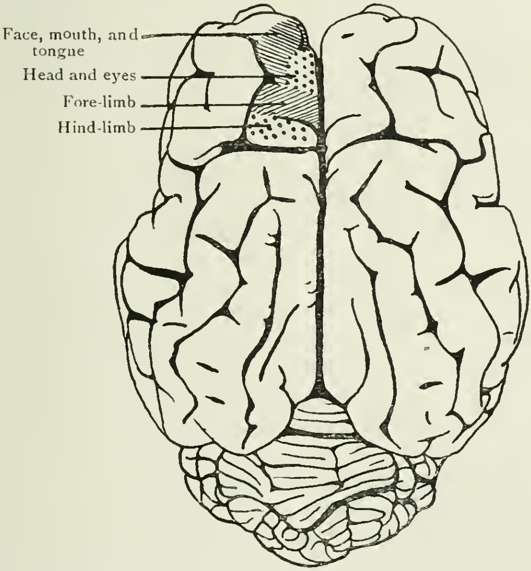

Fig. 159.—Diagram showing Position of Motor Areas on Dorsal Aspect, Brain of Sheep (Simpson and King).

The motor areas in the horse as determined by Arloing are shown in Fig. 158. As with the sheep, a remarkable feature is their comparative unimportance, which has long been anticipated clinically (see below). We have already seen that the chief outflow of motor fibres from the brain of the sheep, and presumably of other herbivora, has a subcortical origin from the mid-brain, pons, and medulla (p. 500).

The effect of removing the motor areas varies according to the species of animal. In the monkey it results in permanent motor paralysis of hand or foot, but not of parts with less skilled movements—*e.g.*, shoulder or knee. In the sheep, as we have just seen, there is no paralysis. In the dog paralysis is not necessarily produced, and it has been supposed that the basal ganglia are capable in this animal of taking up the duties of the cortex. The destruction which has been observed at times in the cortex of the horse is commonly unaccompanied by any symptoms until shortly before death. Colin draws attention to the difficulty of producing paralysis experimentally in the horse from lesions of the hemispheres. Neither the artificial production of a clot in the falciform sinus nor the introduction of pieces of lead the size of a pea into the convolutions gave rise to hemiplegia. This quite bears out a frequently observed clinical fact, that it is possible for horses to have tumours the size of an egg in their lateral ventricles without exhibiting any disturbance. The writer has seen several such cases, the tumours being of variable size, and the clinical history has never given more than a few days' illness, though the growths must have been forming for a considerable period.

Strong stimulation of the motor areas produces epilepsy. By observing the groups of muscles first affected and knowing the region of the cortex to which they are related, it is possible in man to localise with considerable exactitude the seat of this trouble.

The Sensory Areas.—It will be remembered that these serve the higher senses of *vision*, *smell*, *taste*, and *hearing*, as well as the senses of the lower order, *touch*, *temperature*, and *muscle sense*. The term 'sensory' is employed in its physiological sense. The lower order of afferent impulses are those of which we are generally unconscious. Of muscle sense we are, perhaps, under normal conditions, wholly unconscious; towards the perception of heat and cold the consciousness can be awakened, but these are ordinarily unrecognised unless the stimulation is severe. The areas connected with temperature and muscle senses are situated above the crucial sulcus. The *Centre for Vision* is situated in the occipital lobe, and destruction of the centre, say on the right side, is followed by blindness in the two right halves of the retinæ in those animals where decussation of the optic nerves is incomplete. In those in which it is complete a right-brain lesion leads to a left-eye blindness. We shall deal again with this centre in considering the subject of vision. The *Auditory Centre* has been located in the temporal lobes, and the facts connected with it will be considered in the chapter on hearing. The auditory and visual centres are capable of eliciting a response in the motor areas, for the ears are pricked, and the head and eyes turned towards an object or a sound, and therefore connecting paths between the special sense centres and the regions in the motor area, connected with the muscles in question, are believed to exist. *The Olfactory Centre:* In animals with the sense of smell acutely developed the olfactory bulb and tract are large. The dog, rabbit, horse—in fact, most, if not all, of the domestic animals—have the sense of smell highly developed. It is not necessary here to consider the reason in detail, but it is obvious that in the natural state the whole question of their lives hinges largely on the question of smell; food, the presence of an enemy, sexual instinct, are capable of exciting in the cortex psychical reactions, which, in the higher animals, are brought about through other channels. In the primitive brain, swellings first develop in connection with smell, and in the process of evolution the cortical centre for smell was one of the first to be established. In the brain with no cerebrum—as, for instance, in the brain of the shark—the olfactory centre, contrary to the general rule in fishes, is immensely developed. Fishes have excellent sight, but generally no sense of smell; but the shark lives by the sense of smell, and in the old type of brain with which it is furnished the olfactory nerves spread out into an area of considerable size. In the new type of brain—viz., one with cerebral hemispheres—the olfactory lobes form the principal part of the earlier structures, and it is noteworthy that their fibres pass direct to the cortex; all other paths connected with special sense organs have first to pass through the corpus striatum. In man, who has a poor sense of smell, they have atrophied, and in the whale they have practically disappeared. The cortical centre for smell lies in the region of the hippocampus and temporal lobe, but the central connections of the olfactory apparatus are not fully known. The *Centre for Taste* is ultimately mixed up with that of smell, but its precise locality is unknown. With the *Centre for Speech* we have nothing to do. It is interesting to know that stimulation of the corresponding area in the ape does not lead to the production of voice.

When the sense and motor areas are removed from the cortex, there is a considerable amount of substance left not associated with either of these functions. These have been termed by Flechsig *association areas;* the term *silent areas,* employed by some physiologists in speaking of them, appears especially suitable to veterinary physiology. These association or silent areas are the region of the higher intellectual faculties, the organs of thought, the region in which impressions conveyed to the sense centres are interpreted, for it is through the sense centres that intelligence is developed. An association area in the anterior part of the frontal region of man is an important intellectual centre, though of secondary importance to one situated in the parietal region posterior to the fissure of Rolando.

It will be observed that up to this point the functions of the various parts of the cerebrum have been largely determined by direct experiment or pathological observation. These, however, as we indicated previously, are not the only methods of inquiry open. Flechsig's embryological method has furnished important results. It will be remembered that it is based on a knowledge of the periods at which the fibres in the various tracts acquire their medullary sheath. In the human embryo the nerve-fibres are sheathed three or four months after the axis cylinder is formed, and the order in which this occurs appears invariable. The afferent fibres are first myelinated, then the efferent, and lastly the association fibres; this holds good for the nerves of the whole body. At birth the human infant has the afferent system myelinated, but not all the efferent. This, of course, does not apply to those animals which are born with the power of locomotion, but the matter is deeply interesting; also the fact that the functional activity of nerve tracts is largely dependent on the amount of myelin present. In man the myelination of the fibres of the brain goes on for years after birth, but ceases at forty, and in old age diminishes. We have indicated but briefly the field which awaits the veterinary histologist of the future; in the absence of direct experimental inquiry—which nothing can supplant—important information may be gained by an application of the methods of Flechsig.

Function revealed by Structure.—The development of nervous tissue from its earliest laying down to its maturity has, as we have seen, been turned to account in the interpretation of its function. The next step, on somewhat similar lines, was the interpretation of function by a comparison of the structure of the various parts of the cortex in normal and insane persons. Of the structure of the cortex an outline has already been given; the four, or, as some prefer, six, layers of cells and fibres into which this has been divided have been given another classification by Bolton,* which has been generally adopted. It is spoken of as the five-layered type of cortex, and the following are described in man:

1. *Outer fibre lamina*: Two-thirds developed at birth.
2. *Outer cell lamina*: Half developed at birth.
3. *Middle cell lamina*: Three-fourths developed at birth.
4. *Inner fibre lamina*: Two-thirds developed at birth.
5. *Inner cell lamina*: Fully developed at birth.

Watson† has studied the development of these layers in many orders of mammals. He shows that layers 4 and 5 are the earliest to appear, and whether in the highest or lowest mammals there is very little difference in their thickness (Fig. 160). Layer 3 is the next in order of development. Layers 1 and 2 are the last to appear, and the slowest in development. In the lowest mammals layer 2 is generally poorly developed, and even at best obtains but a slight absolute depth as compared with the human brain.

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* 'Further Advances in Physiology,' edited by L. Hill, M.B., F.R.S. Goulstonian Lectures, J. S. Bolton, M.D.: *Brain*, part cxxix., vol. xxxiii., 1910.

† 'The Mammalian Cerebral Cortex, with Special Reference to its Comparative Histology,' G .A. Watson, M.B., C.M., *Archives of Neurology*, vol. iii., 1907.

The great difference between the human brain and that of the insectivora lies chiefly in the degree of development of layer 2, whereas, notwithstanding the difference between the brain of man and that of the mole—one of the smallest in the mammalian series—layers 3, 4, and 5 are of much the same thickness (depth) in each animal. Fig. 160 illustrates approximately the relative depths of the cerebral cortical layers in the normal human adult and the mole (after Watson). From the point of view of intelligence, layer 2 is of the utmost importance; it is under-developed to different degrees in idiots and imbeciles, and in chronic and recurrent lunatics the same fact is observed, though in a lesser degree. The examination of the various layers of the cortex in cases of congenital blindness has shown that certain portions of layer 3 are atrophied; this has enabled the cortex to be mapped out into a projection centre for visual impressions, known as the *visuo-sensory area*. At the peri-

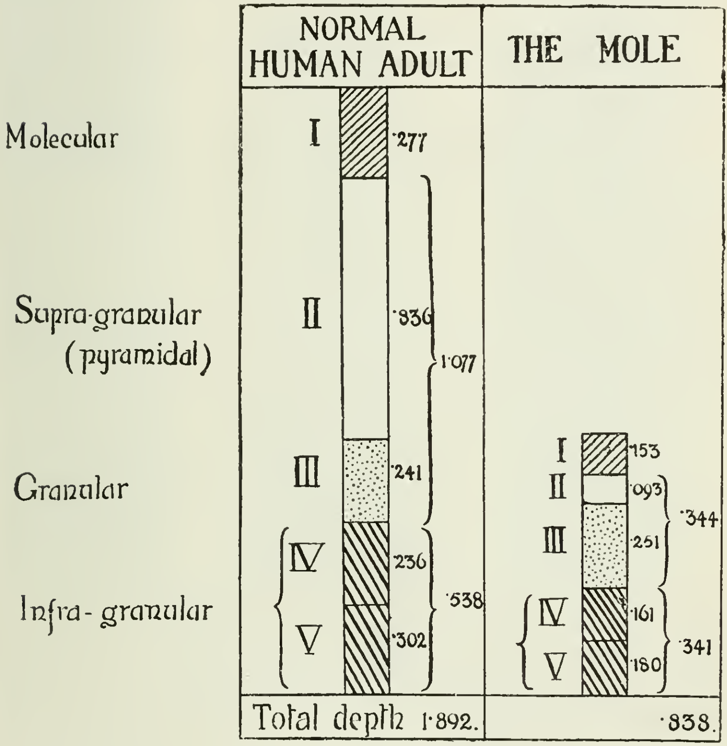

FIG. 160.—THE APPROXIMATE RELATIVE DEPTHS OF THE CEREBRAL CORTICAL LAYERS IN MAN AND THE MOLE (WATSON.)

phery of this area is another, which can be distinguished by an abrupt modification in the arrangement of the layers. It is known as the *visuo-psychic*; it undergoes no change in congenital blindness, and therefore has no visuo-sensory function. The visuo-psychic layers are not affected in dementia. A third region of the cortex is the *prefrontal*; it is the last to reach maturity, and is the region specially affected in mental disease. Its cell layer, No. 2, has been previously referred to as showing marked retrogressive changes in mental affections. Layer No. 2 is the most important of the human brain, and it is the only one which varies in depth in normal individuals.

The functions of the cell laminæ of the cortex, according to the observers previously mentioned, and generally accepted by neurologists, are as follows:

Layers 1 *and* 2 carry out the *psychic*, or associational, functions of the cerebrum; they represent educability and general intelligence. Hence they are rudimentary in the insectivora, better developed in rodents, again better developed in ungulates and carnivores than in rodents, and markedly more developed in the primates than in the carnivores. They have to do 'with all those activities which it is obvious the animal has acquired (or perfected) by individual experience, and with all the possible modifications of behaviour which may arise in relation to some novel situation; hence, with what is usually described as indicating intelligent as apart from instinctive acts, the former being not merely accompanied, but controlled, by consciousness' (Watson). The region of the brain where these processes are carried on is mainly in the prefrontal, or region of higher associations. Of less importance in this respect is the visuo-psychic, or region of lower associations; and of least importance is the visuo-sensory or projection-sphere region. *Layer* 3 deals with the reception or transformation of afferent impressions, whether from within or without the brain. *Layers* 4 *and* 5 govern the lower voluntary and instinctive activities of the body, which require neither experience nor education. They deal with the preservation and perpetuation of the species, with such things as food, shelter, and sexual consort, accompanied, though not necessarily controlled, by consciousness. Preservation is deeply, firmly, and early implanted in the brain of the lowest mammals, and in them is as fully developed as in man. It is the common platform on which they meet man. In Fig. 161 is shown the microscopical structure of the Betz-cell area in man and the dog, and the motor area of the pig, the depth of the laminæ in each case being indicated.*

Coverings of the Brain.—The dura mater is a dense fibrous membrane, which acts the part of a protective covering for the brain; between it and the arachnoid there exists a lymphatic space known as the subdural. The arachnoid contains but few vessels and no nerves, and covers the extremely vascular pia mater; between the arachnoid and the pia mater is formed the subarachnoid space, which contains the subarachnoid or cerebral fluid.

Cerebral Fluid.—The cerebral fluid is secreted by the pia mater and choroid plexus; in horses it is normally small in

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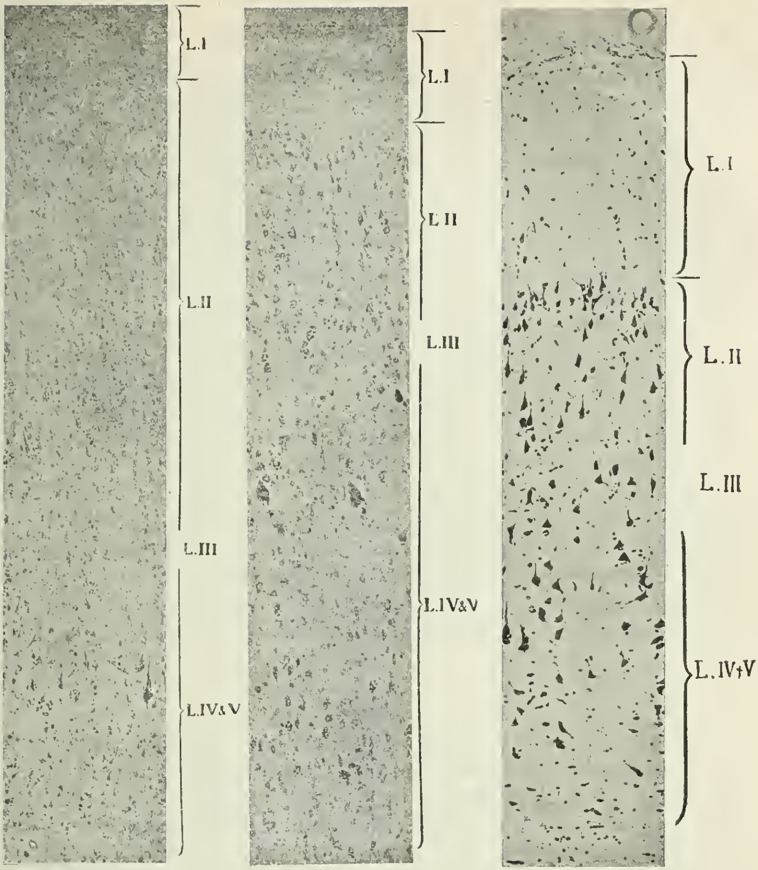
* For these I am indebted to Dr. G. A. Watson. The structure of the cortex of the brain of the pig had not previously been investigated.



(1) Man.
× 74 diameters.

(2) Dog.
× 89 diameters.

(3) Pig.
× 109 diameters.

Fig. 161.—Cortex of the Betz Cell Area of Man and of the Corresponding Areas in the Dog and Pig (Watson).

The magnification of (1) is less than that of (2) and (3). The depth of the different layers of the cortex is approximately indicated by the markings to the right of the figures.

In man, L.II.—the pyramidal lamina—is much the best developed layer of the cortex, being considerably deeper than the conjoined layers III. to V. It is the lamina of 'psychic, associative, and educative significance.' In the dog and pig, L.II. is comparatively poorly developed, having a depth of only one-third to one-half of the conjoined layers III. to V. The conjoined layers IV. and V., which are of 'organic and instinctive significance,' are of more nearly equal depth in all three specimens. In this region L.III.—the granule or receptive lamina—is reduced to a minimal depth and distinctness in all the cortices. L.I.—the outer fibre lamina—is relatively deep in the pig, possibly owing to a failure of development in the upward direction of the pyramidal layer.

The larger cells of L.IV. in the 'motor' area of the pig have not the characteristic shape and appearance of the Betz cells of the human motor cortex; the corresponding cells in the cortex of the dog more nearly approximate to the human type.

In the cortex of the pig the individual nerve-cells, though fewer in number than in the dog, have a less embryonic appearance.

quantity, amounting to about 5 or 6 grammes (80 or 90 grains). The use of this fluid is to equalise the pressure on the brain, and to afford protection to it; by the manner in which this organ is suspended inside the skull by the dura mater it is saved from jar and concussion. Both cerebrum and cerebellum half float on water-cushions. Withdrawal of the cerebral fluid leads to convulsions, while an increase in the amount may cause coma, owing to the pressure exercised. When the arteries in the brain dilate, the skull being unyielding, some room is made for the extra blood by displacement of the cerebro-spinal fluid.

Halliburton's researches have shown that the cerebro-spinal fluid is constantly being secreted, and as constantly got rid of. Its channel of exit is not by the lymphatic system, but by diffusion into the blood-stream. This fluid takes the place of lymph, though it is a true secretion, and not in part an exudation as lymph is. There is an abundant exchange between the cerebro-spinal fluid and blood, but very little, if any, between the blood and cerebro-spinal fluid. Halliburton regards this fluid as an ideal physiological saline, in which the sensitive neurones are bathed in order to obtain their osmotic equilibrium.

Movements of the Brain are dealt with at p. 99.

Sleep.

The actual cause of sleep is not known. The tissues require rest and repair, and these are undoubtedly effected during sleep; but no explanation which has been generally accepted has accounted for the loss of consciousness which occurs during the process of anabolism. The amount of sleep required by animals appears to be greater in the carnivora than the herbivora. The dog and cat spend a considerable time in this condition of unconsciousness, but the herbivora sleep much less, and for only short periods at a time. Neither class sleep with the same depth nor intensity as man; it is not conceivable that a dog or cat could remain in a condition of profound slumber while considerable noise was occurring. In the case of the horse he is such a light sleeper that the faintest footfall suffices to wake him up. He sleeps with his eyes open or semi-open and on his side, fully extended. The ruminant sleeps resting on the chin, with the head extended, or with the nose turned in to the side. The horse sleeps for short periods together; his immense weight does not admit of his lying for any length of time on one side, for during this period the lower lung does no work and the lower muscles get cramped. He rises and lies on the opposite side, or rolls over to that side; or may rise, eat for a short time, and again lie down. He requires little sleep, but it should be of good quality. Hard-worked horses cannot do without it. The horse has the power of sleeping while standing, for which the limbs are provided with certain necessary mechanisms in connection with the muscles, which will be examined in the chapter on locomotion. The horse that sleeps while standing drops the head below the level of the withers, the eyelids partly fall over the eyeball, and the limbs are brought rather more under the body than usual. The extensor muscles of the limb cannot be relaxed, or the body would fall (p. 435); they must accordingly continue to have impulses poured into them in order to maintain their contracted condition. Nor is this confined to the limb muscles; those which sling the body between the fore-legs must also have tone imparted to them if the erect attitude is to be maintained. The impulses dealing with body equilibrium must also continue in operation. None of the mechanisms of the limbs which aid the muscles and tendons are in any way adequate to explain these facts. The extensor muscles, on which everything depends, receive assistance from the fascia of the arm and thigh. The muscles themselves are extremely powerful, and possess in their substance a large amount of tendinous material, such as is evident in all muscles constantly in action—for example, those of the back, masseter muscles, and others. During sleep the horse is unconscious, and the muscles are under no kind of cerebral control, yet they remain strong and in operation without the knowledge of the animal. This is due to the reflex actions of the spinal cord, which, as has previously been urged, are so evident in the herbivora (p. 478); likewise the reflex control involving the cerebellum is still in full operation in maintaining posture, so that, asleep or awake, through these agencies, the tonus of the muscles is maintained, not only of the limbs, but of the back and chest wall, which are equally essential to the maintenance of the erect attitude. The attitude of the sleeping bird, on one leg, is a similar instance of the maintenance of reflex balance when consciousness is in abeyance.

The rest obtained by sleeping in the erect attitude is insufficient for hard-worked horses. They need the complete relaxation of their muscles, and this can only be furnished in the recumbent position. When from anchylosis of the vertebræ or other causes the horse does not lie down, he must be placed in slings at night in order to obtain the needful rest. If not hard worked, they may stand for years without this aid; on board a ship, or for surgical reasons, they may be kept in a confined position for a considerable period without lying down, especially if the muscles be exercised for a few minutes each day. Horses are not free from falling when asleep; they may even actually come to the ground, but this is rare; what generally happens is that relaxation of the extensors of the fore-limbs occurs, and the animal knuckles over on to the fetlocks and at once recovers itself, but not without inflicting an injury to the skin over the joint. The fall always occurs in front, and not behind; probably the extra weight on the fore-legs may have something to do with this.

Observations made on man and those animals which lend themselves to inquiry show that during sleep the respirations become slower and deeper, and this can readily be observed in the horse. The secretion of urine becomes lessened, the pulse-rate and blood-pressure fall, and the brain shrinks, so that the volume of blood in the other parts of the body is slightly increased, as might be expected from the general inaction of the muscles. The production of carbon dioxide is lessened, while the loss of nervous control over the production of heat causes a fall in temperature. The essential physiological factor in sleep appears to be the anæmia of the brain.

The Theories of Sleep.—The theories formed to account for sleep may shortly be stated. One is based on the *accumulation of acid waste products* in the system. The source of these lies mainly in the muscles. These tissues, as we have already seen (p. 444), are capable of producing lactic acid. Lactic acid injected into the circulation is said to produce fatigue, and it certainly produces unconsciousness. Sleep after severe muscular work is a necessity, but the acid theory is obviously incomplete, or the idler would need but little sleep. The *doctrine of the neurone* has been evoked to explain sleep, the suggestion being that the synapses in the cells of the cerebral cortex shrink, and in consequence fail to make connection with the incoming fibres from the outside world. The view has been put forward by Salmon* that sleep is presided over by an organ of internal secretion. The secretion, he considers, is furnished by the cells of the cerebral cortex.

Hibernal Sleep.—The long period of sleep enjoyed by hibernating animals appears to be protective in character, and represents the tiding over of a period when food-supply is defective. A study of the processes which attend this remarkable phenomenon might be expected to throw some light on the cause of ordinary sleep. It can hardly be urged that in this case the cerebral cells are secreting a substance, which keeps the animal in a state of such profound sleep that evidences of life have frequently to be carefully looked for. The metabolism occurring during hibernation has been referred to at p. 416. Salmon draws attention to the remarkable activity occurring in the *hibernal gland*. This gland lies beside the thymus, and when stored may reach the whole length of the body. It is highly vascular and charged with a fatty substance, rich in lecithin, which accumulates during the summer and is consumed during the period of sleep, so that at the end of the winter the gland, like the animal, may be a mere shred. This gland contains a colloid substance, and it is significant that a similar material is found in the blood of hibernating animals and in no others. No definite statement can, however, at present be made as to whether the gland furnishes the sleep-inducing material as well as the food-supply.

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* *British Medical Journal*, July 8, 1911.

Psychical Function.—In attempting to define to what extent the faculty of reasoning exists in animals we are treading on distinctly controversial ground. Probably this question can be positively answered in the affirmative for two animals only—namely, the elephant and the dog. In the horse the moral sense* is very small; we do not think he knows he is doing anything wrong when he periodically kicks his stable into matchwood, or when he 'runs away,' but he understands that he should not refuse a jump, and a horse careless in his walk or trot knows exactly what every stumble will be followed by, and anticipates matters accordingly. Strength of will most animals lose as the result of domestication. They become mere reflex machines or automata, but there are notable exceptions—for instance, the ass, mule, and occasionally the horse. The so-called stupidity of the ass and provoking obstinacy of the mule are not indications of want of intelligence; on the other hand, these animals show a determination of purpose and strength of will, which, it more deeply marked and combined with aggressiveness, would keep them as free from civilisation as the zebra. The majority of horses, on the other hand, have no great strength of will; they can be rendered docile and tractable, they will gallop until they drop, work at high pressure when low would suffice, can never apparently learn the obvious lesson that it is the 'willing horse' which suffers, and that the harder they work the more they get to do. All this is due to defective intelligence and a want of the higher faculties; they cannot reason† like the dog or elephant, and are more flexible than the ass or mule. Some horses show signs of reasoning and are capable of grasping a position. A load so heavy as to be beyond the limit of his power, or some other cause, has taught him to refuse to work; to use the familiar expression, he 'jibs,' he has learned to disobey, he has learned his own strength, and the comparative powerlessness of his master, and this through an exercise of reason. In other words, the horse which refuses to wear himself out in the service of man is one possessing too much intelligence and strength of will for a slave; a 'jibber' is an intelligent and not a stupid horse. As a rule, the intelligence and affection of the horse exist only in books and in the imagination of those who have least to do with him; in whatever region of the brain affection is located, it does not occupy much space in the equine. Taking the dog as the standard to judge by, it may he said with the greatest truth that the large majority of horses have no affection whatever, either for their own kind (excluding maternal affection) or for human beings. There are exceptions; a kind groom is appreciated, and a pair of horses may become greatly attached, or a horse may become very fond of a cat. The liking of mules for the grey mare which leads the troop is well known. Nevertheless, two strange horses cannot as a rule be put together without disagreeing, and no one ever heard of a horse pining away through the prolonged absence of his master. The often-quoted example of a horse jumping over a man on the ground rather than treading on him is an act misunderstood; it is true the horse jumps over the man, but he does so because he is taught to jump over every obstacle, and the man on the ground might, for all he knows, be a bush. In other words, it becomes largely a reflex, and only to a very limited extent a volitional act. If the leading members of a flock of sheep are made to jump over an obstacle, and the obstacle then be removed, all the succeeding sheep will continue to jump on arriving at the same spot.

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* The use of this term is open to objection in the case of animals, but it appears to the writer that something equivalent to the moral sense does exist in them. The expression on a dog's face when he has done something he knows to be wrong, or, at any rate, which he knows is against the rules laid down for his life, conveys a conception of the existence of moral sense.

† Exception may be taken to the employment of the term 'reason.' To reason is impossible without general concepts, and in the absence of speech general concepts are difficult to suppose. Nevertheless, the term is convenient, especially as the writer considers that the more intelligent of the lower animals possess what in them amounts to reasoning power.

The absence of speech suggests that animals have no power of intercommunication. The question cannot be discussed here, but those concerned in closely watching the habits of animals must frequently feel that communication between them is not impossible.

If the horse possesses but little affection, this defect is compensated for by his cherishing no ill will; to all his hard life and the abominable cruelties of domestication he shows no sign of resentment; water and feed him, and give him a place to lie in, and he forgets the past in his anxiety for the present. He is a peculiar mixture of courage and cowardice; physical suffering he can endure, no animal bears pain better; when his blood is up nothing is too big or too wide for him in the hunting-field, and he has a keen enjoyment of both chase and race in spite of the punishment they may entail. But the same horse is frightened out of his life by a piece of paper blowing across the road, or by his own shadow, and an unusual sight, or a heap of stones on the side of the road has cost many a man his life. No animal is more readily seized with panic, and this spreads amongst a body of horses like an electric shock. Yet panic must not be held to indicate an absence of reason, though the rapidity of its spread in the case of a stampede may suggest it. There are other animals than the horse affected by panic. The dog, with all his intelligence, is acutely affected by a pot tied to his tail, but it does not cause all the dogs he meets to stampede. Panic is not unknown in the highest animal, and reason does not prevent it.

Reasoning power in the majority of horses is very small; an animal runs away because he is seized with panic, or because his spirits are bubbling over. Yet he has sufficient reasoning powers to learn that for the time being he was master of the situation, and if intelligent above the average he becomes a confirmed 'bolter.' Distinct acts of reasoning are rare; of the lack of these we daily see examples in our hospitals—namely, horses injured in the most severe manner through their own struggles when placed in a little difficulty, such as a head rope around the leg, or an inability to rise when down, owing to being too close to the wall, or some trifling circumstance of this kind. In these difficulties, if he employed any reasoning powers he would remain quiet until released, instead of which he behaves like a lunatic, inflicting on himself in a short time injuries which may lay him up for months. Or take the case of a horse which gets his tail over the reins when being driven; instead of lifting the tail in response to the exertions of the driver, he draws it closer down to his quarters, gripping the reins as in a vice, and is so astonished and frightened at the new state of things that he becomes uncontrollable. We can hardly point to a single act in the horse in which the powers of reasoning are clearly brought into play, unless it be that he knows punishment follows refusal to obey, and that he often learns to 'jib.' Further, he recognises in a moment whether the man on his back intends to be master, or is somebody with whom he can trifle. Every horse knows a truss of hay or straw by sight. The point need not be laboured, yet no horse will pass a truss of either lying in the road. He appears unable to reason that what he is familiar with in the stable may be no more dangerous when met with in an unusual situation.

The horse is very conservative; he does not like anything new or any departure from his ordinary mode of life; he will starve himself for days rather than take a new feeding grain. He will not at first drink out of a trough if he has been used to a bucket or stream, and he dislikes a change of stable or a new place. His gregarious instincts are proverbial; he frets at the absence of his companions, and if used to work amongst a body of horses, as in cavalry, he will take any degree of punishment rather than leave them for a few minutes. During the absence of his companions he neighs, sweats, paws with the fore-legs, and almost screams with delight on rejoining them, not because he loves them, but because he dislikes being alone.

The horse has an excellent memory for locality, probably nearly equal to that of the dog or cat; he never forgets a road, and, automaton-like, if he has once stopped at any place on it, he wants to stop at the same place next time, no matter how long the interval may be between the visits. Finally, his predominant feature, and the feature of all animals below adult man, is the childishness present throughout life; probably the absence of care, worry, and anxiety may account for this. The horse will play all day with a piece of rope, or nibble his neighbour persistently; even the oldest horses, when 'fresh,' will perform the antics of a foal, and imitation amongst them is so universal that, if one of a string of horses being led along happens to kick out, this repeats itself all along the line as if by preconceived arrangement.

Sydney Smith defined the difference between reason and instinct as follows: 'If, in order to do a certain thing, certain means are adopted to effect it, with a clear and precise notion that these means are subservient to that end, the act is one of reason; if, on the other hand, means are adopted subservient to an end, without there being the least degree of consciousness that these means are subservient to the end, then the act is one of instinct.' L. Morgan* believes that between instinct on the one hand, and reason on the other, we may insert as a middle term 'intelligence,' while Romanes† and others use the word 'intelligence' as synonymous with 'reason.' Morgan defines instinct as a motor response to a certain stimulus—*i.e.*, a reflex act, but one accompanied by consciousness. Animals come into the world endowed with this innate capacity for motor response; but these instincts are not quite perfect; they need training and experience, and their instructor is 'intelligence.' Intelligence, according to this authority, does not imply a conscious knowledge of the relation between the means employed and the end attained; such a conscious knowledge would be reason. In other words, we are to regard animals as simply reflex machines, their brain being very little higher in function than their spinal cord, and in respect of some, but certainly not of all, such a position is tenable. Morgan's definition of instinct and intelligence offers no reasonable explanation of why a dog buries a bone, or why they fight or worry cats; nor does it explain why a horse sq inclined will turn his quarters towards another as he passes, and rapidly let both hind-legs fly in the direction of his objective; nor why he uses his fore-legs to strike when he knows his hind-legs cannot reach the object of his irritation. It fails completely to explain why an elephant employed piling timber refuses to work one minute beyond the allotted hours. Nor can we believe that the extraordinary sense shown by a sheep-dog is not directed by reason. It is absolutely impossible to believe that such acts as we refer to imply no conscious knowledge of the relation between the means employed and the end attained.

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* *Fortnightly Review*, August, 1893; 'Habit and Instinct,' 1896.

† 'Animal Intelligence,' 1883; 'Mental Evolution in Animals,' 1883.

The higher animals are capable of a limited amount of reasoning; in some the faculty is even relatively well developed, with others it is extremely imperfect. The elephant and dog are here at the top of the scale, the ox and sheep at the bottom, the horse comes midway. We do not see how to separate reason from intelligence, but there is no difficulty in separating these from instinct.

Lord Avebury, in one of his lectures on 'The Senses and Intelligence of Animals,' drew attention to the fact that in spite of the wisdom and cleverness of the dog, there was much doubt as to whether he could realise that two and two made four, though he could be taught to call attention to his daily needs by picking up cards bearing certain words as 'food,' 'water,' 'door'; the same animal could not, however, be taught to bring the duplicates of cards having distinctive colours or marks.

Avebury remarked that he had always felt a great longing to know how the world appeared to animals. It seems impossible to believe that their minds are a blank. A dog in search of his master has his mind occupied, and as during sleep he dreams, it is evident that the thoughts which have passed through it have left an impression. Even with the horse it is not possible to believe that daylight and darkness, food and water, work and rest, form the only subjects of thought as they present themselves. The whole question bristles with difficulties, and, as Avebury says, we have tried to obtain information of the senses and intelligence of animals by teaching them our ideas, rather than devising a language or code of signals by means of which they might communicate theirs to us.

Some animals are born with such complicated reflex acts as walking, galloping, jumping, etc., so highly developed that they are employed at once. No member of the human family has been seen to walk and run about a few hours after leaving the womb, for both brain and spinal cord are incompletely developed, and the acts have to be learned. This is not so with animals (excepting the dog and cat): the chick walks out of its shell, foals, calves, lambs, goats, etc., are born prepared to feel their feet at once; they require no teaching and exercise no imitation, their senses are perfect, they can recognise their mother or a stranger, can see, smell, hear; in fact, they have nothing to learn, for they are born with as much intelligence as their parents, and differ from them in one respect only, and that is, they are born wild, and so have to learn confidence. Domestication and obedience are not properties transmitted from parent to offspring.

'Thinking Horses.'— Some years ago extraordinary interest was aroused by the report that some horses in Germany had been taught to think. A mathematical master, Von Osten by name, discovered that the horse he drove responded intelligently to verbal instructions, such as 'Turn to the left—or right,' and he succeeded in a short time in driving this animal by spoken directions only through the crowded thoroughfares of Berlin. This horse died, and was replaced by one which was put through a regular course of instruction in arithmetic and spelling. Von Osten now came in contact with one Krall of Elberfeld, who knew nothing whatever of horses, but was nevertheless convinced that the animal belonging to Von Osten was genuinely intelligent. He accordingly purchased two Arab stallions, which were given a course of elementary school instruction, and he obtained results much higher than those of Von Osten. They were taught the first four rules of arithmetic, and then more complex problems, such as the extraction of the square root. Spelling was also taught. The horse then began to spell out spontaneous statements, and in these a phonetic system was employed—for instance, 'essen,' to eat, was spelt 'sn,' and 'gehen,' to go, 'gn.'

The Society for Psychical Research in this country attempted to discover the explanation of these extraordinary results, but their investigation led to nothing. The report was published in *The Times* of 4th July, 1913, and on this we have drawn. Several Commissions had sat in Germany with equally negative results.

The general impression was that the animals worked by signals given consciously or unconsciously by the trainer, or someone present, but from a letter to *The Times* of 19th June, 1914, it appeared that a blind horse had been educated, and was thoroughly reliable in his answers. The problem accordingly has never been solved.

It must be evident from the views expressed by the writer in his account of the intelligence of the horse that he regards the performances of the 'thinking horses' of Germany as dependent on a skilful deception.

SECTION 7.

The Cranial Nerves.

There are twelve pairs of cranial nerves; of these two only are required to take part in functions other than those connected with the head. This leaves ten pairs, the function of which is wholly connected with the head, either as nerves of special sense, or in a motor or sensory capacity.

Modern Classification of Cranial Nerves.

The modern theory of the architecture of the cranial nerves conceives them as built on the same lines as spinal nerves. In this scheme the first and second pairs are not included, the olfactory bulb and retina being regarded as outgrowths from the brain. From the third pair to the twelfth the cranial nerves originate from the brain stem—*i.e.*, the bulb, pons, and mid-brain—which is only an extension forward of the spinal cord. Scattered irregularly in this position, but mainly in the region of the fourth ventricle, are groups of nerve-cells, or nuclei, some of which are sensory, others motor. The motor nuclei are arranged in two longitudinal rows on either side of the primitive neural axis. From the median row arise the third, fourth, sixth, and twelfth nerves; from the lateral row the motor branches of the fifth, seventh, ninth, tenth, and eleventh.

Nuclei which have been termed sensory are found in the same region connected with the fifth, eighth, ninth, and tenth nerves. These nuclei are the terminations of the sensory cranial nerves, which are arranged in the same way as the spinal nerves, and have ganglia on their sensory roots. The cranial nerves with their ganglia are outside the cranial cavity. The ganglia consist of cells, each, like a spinal nerve ganglion, possessing a **T**-shaped process, one end of which grows to the centre, and one to the periphery. It is the central end of the **T**-piece which terminates in the sensory nucleus of the brain stem by arborising around its cells. It will be observed that the sensory fibres do not arise in the nuclei, but terminate there. The resemblance between the cranial and spinal nerves is completed by the existence of sympathetic fibres in the cranial system.

In this scheme the sensory portion of the fifth pair is represented by the dorsal roots of the following motor (ventral) cranial nerves—*i.e.*, seventh and twelfth. The tenth pair becomes the dorsal root of the eleventh. The ninth becomes a dorsal, with no ventral root. The eighth nerve has its dorsal root from the cochlea, and its ventral from the vestibule and semicircular canals.

The special senses for which provision is made are *smell, sight, hearing,* and *taste.* Only two of these senses—viz., smell and sight—have nerves exclusively devoted to their functions;

the senses both of hearing and taste are furnished by nerves which perform additional functions:

The afferent cranial nerves are:

First, or olfactory.
Second, or optic.
Eighth, or auditory.

The efferent nerves are:

Seventh pair: Motor to the muscles of the face.
Eleventh pair: Motor to the muscles of the neck and shoulders.
Twelfth pair: Motor to the muscles of the tongue.

Mixed nerves:

Third pair Fourth pair Sixth pair	Motor and sensory to the muscles of the eyeball.
Fifth pair Ninth pair Tenth pair	Resemble spinal nerves in consisting of a motor and a sensory root, with a ganglion on the latter.

Afferent Group.

The nerves of special sense will be dealt with in the chapter devoted to the senses.

Efferent Group.

Seventh Pair, or Facial.—This nerve has been grouped as efferent, but in its course it receives sensory fibres, though at its origin it is exclusively motor. It arises from the medulla behind the pons, at the lateral part of the corpus trapezoides. The deep-seated origin is from the facial nucleus in the medulla. In company with the eighth or auditory pair, it passes through the internal auditory meatus, but escaping from the internal ear by the aqueduct of Fallopius, it leaves the eighth nerve, and passing beneath the parotid gland, finds its way to the face, about 1½ inches below the articulation, over the external masseter muscle. During this short course the nerve has supplied the small superficial petrosal nerve, a nerve to the stapedius muscle of the middle ear, and the *chorda tympani*. The latter takes a remarkable course through the petrous temporal bone; emerging, it supplies secretory fibres to the submaxillary and sublingual glands, and eventually joins the lingual nerve of the fifth pair, and is distributed to the anterior two-thirds of the tongue. Besides the above branches, the main trunk of the facial, on its way to the face, has supplied motor fibres to the muscles of the external ear, and sensory fibres to the skin of that part; motor fibres to the digastric muscle, to the orbicularis of the eye, and the corrugator of the brow. The main trunk on the surface of the masseter muscle divides into two branches, which between them supply all the muscles of the face, lips, cheek, and nostril with motor power. *The seventh nerve is the nerve of expression.* In this connection it supplies the external ear and all the muscles of the face and lips. Paralysis of this nerve produces a typical facial expression (Fig. 162). The ear droops, the eye remains open, the upper lip is drawn towards the sound side, is elongated and flabby; the lower lip droops, and saliva runs from the mouth; the nostrils are elongated, and the face possesses a stupid, vacant look. Nutritive change may occur to the eye in consequence of exposure, and deafness is present owing to paralysis of the muscle of the middle ear. Bernard pointed out that if both facial nerves be divided in the horse, and the animal galloped, suffocation results in consequence of the nostrils being unable to dilate, and the horse unable to breathe through the mouth. Though the facial is intimately connected with the masseter muscle, as may be seen in the face of a well-bred horse, no motor fibres are supplied to this, nor, in fact, to any of the principal muscles of mastication; it does, however, supply fibres to the stylo-maxillaris, in part to the digastricus, and to two small muscles connected with the hyoid bone.

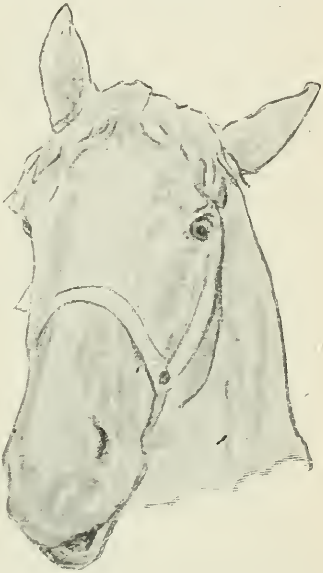

FIG. 162.—CHARACTERISTIC FACIAL EXPRESSION OF THE HORSE WITH PARALYSIS OF THE SEVENTH NERVE.

The seventh pair of nerves in all animals control the muscles of expression, of emotion, pain, and pleasure. In the horse they are in addition respiratory nerves of the first importance, as they control every movement of the nostrils.

Eleventh Pair, or Spinal Accessory.—This is a purely motor nerve, with two roots of origin—viz., the bulb and the spinal cord as low down as the fifth cervical vertebra. This latter branch passes up the cord between the motor and sensory roots, receiving filaments on the way, and entering the foramen magnum it joins the root arising from the bulb. It leaves the skull in company with the vagus; then, separating from this nerve, it divides into two branches, which supply the sternomaxillaris, levator humeri, and trapezius muscles with motor power.

This nerve furnishes motor fibres to the vagus, and is connected with the superior cervical ganglion of the sympathetic (see p. 559). Its course is very remarkable; having run all the way up the neck within the spinal canal, its dorsal branch passes externally down the neck as far as the upper part of the scapula, and its object in doing so is to innervate the trapezius. It passes other large muscles of the neck, such as the splenius, without supplying them with any fibres, while all the muscles in the neighbourhood of the trapezius are supplied with motor power direct from the spinal cord.

Owing to its connection with the vagus nerve, division of the accessory causes loss of voice. Bernard showed that crowing in birds was no longer possible after dividing the root within the spinal canal.

The **Twelfth Nerve, or Hypoglossal,** is the motor nerve of the tongue. It is the last cranial nerve to arise from the medulla, which it does by means of several filaments. The deep-seated origin is the hypoglossal nucleus, which is situated in the floor of the fourth ventricle, near the mid-line. The nuclei of both sides are connected by fibres. On its passage to the tongue this nerve establishes connection with the first cervical and the superior cervical ganglia of the sympathetic, and subsequently supplies all the muscles of the tongue, with fibres to those muscles which depress the larynx.

Mixed Group.

This group, it will be remembered, resembles spinal nerves in consisting of a sensory and a motor portion, the fifth, ninth, and tenth pairs possessing a ganglion on the sensory root.

Third Pair, or Motor Oculi.—This nerve has a deep-seated origin in the *anterior corpora quadrigemina* and *peduncles of the cerebrum.* It supplies with motor power all the muscles of the eyeball, including the retractor and muscle of the upper lid, but does not supply the *external rectus* nor the *superior oblique.* Through its connection with the ciliary ganglion it supplies fibres to the sphincter of the iris and to the ciliary muscle (see The Eye). At its origin this nerve is connected with the two other motor nerves of the eyeball—viz., the fourth and sixth pairs. Division of the third pair causes the eye to turn downwards and outwards, owing to the unbalanced action of the superior oblique and external rectus muscles. There is also depression of the upper lid, immobility of the eyeball, and dilatation of the pupil. The sense of direction and the reflex tonus of the eyeball muscles are also conveyed by these nerves. The movement of the eyeball muscles will be considered in detail later.

Fourth Pair, or Pathetic.—This is the smallest cranial nerve. It arises immediately behind the corpora quadrigemina in the anterior cerebellar peduncle. The deep-seated origin is from a nucleus in the floor of the cerebral aqueduct. Sisson* points out that the fibres of this nerve decussate totally in the anterior medullary velum, so that the fibres for the left eye are derived from the right brain. The fourth cranial nerve supplies motor power to only one muscle—viz., the superior oblique of the eyeball.

Sixth Pair, or Abducens.—This nerve arises from the bulb behind the pons, and external to the pyramid. It supplies the external rectus or abductor muscle of the eyeball, a portion of the retractor, and the deep recti with motor power.

A large number of fibres in the third, fourth, and sixth pairs of nerves are afferent, and supply receptive nerve-endings to the various muscles and their tendons. These branches are concerned in the postural action (tonus) of the eyeball muscles (Sherrington).

Fifth Pair, or Pars Trigemini.—The large *sensory root* of this nerve arises from the *pons*, close to the *middle peduncle of the cerebellum*, and at the *foramen lacerum* has upon it a large ganglion known as the *Gasserian*. The deep-seated origin of the sensory root is from the *trigeminal nucleus*, which, according to Dexler,† extends from the pons to the sixth cervical segment of the cord, and is known as the *spinal tract of the trigeminus*. The connections of the trigeminal sensory root in the brain are with the thalamus and cerebral cortex of the opposite side. In ungulates it is also, according to Wallenberg,‡ connected with the thalamus of its own side. Further, it is connected with the motor nuclei of the fifth, seventh, ninth, tenth, and twelfth cranial nerves. The Gasserian ganglion behaves like a spinal ganglion. From its axons the sensory fibres arise which pass outwards to the structures of the face and head, and confer on them ordinary, and, in the case of the lips, acute tactile sense. Fibres passing from the Gasserian ganglion to the brain are linked up, as shown above, with the optic thalamus, the central seat of sensory impressions. The *motor root* arises from the *pons* on the inside of the sensory root. From these two roots three branches of nerve are formed—the *ophthalmic, superior maxillary*, and *inferior maxillary*. The **Ophthalmic branch** is the smallest, and is purely sensory. It supplies the lachrymal gland, upper eyelid, membrana nictitans, temporal region, mucous membrane of septum nasi, and superior turbinated bone, and provides the sensory root of the ciliary ganglion. The **Superior Maxillary Branch** is of great size, and purely sensory in function. It supplies the septum of the nostril, hard palate, teeth, gums, soft palate, upper lip, guttural pouch, parotid gland, external ear, skin, and other structures of the face. The immense bundle which issues from the infra-orbital canal of the horse is out of all proportion to the extent of tissue to be supplied either with ordinary sensation or with tactile sensibility. The **Inferior Maxillary Branch** is a mixed nerve, its sensory fibres being derived from the Gasserian ganglion, its motor fibres from the motor root of the main trunk. It is through the motor fibres of this branch that mastication is carried on—in fact, it has been termed the *masticatory nerve*. It supplies all the muscles of mastication excepting the digastricus. Its sensory fibres are distributed to the lining membrane of the lips and mouth, to the molar and incisor teeth in the lower jaw, and the structures connected therewith, also to the anterior two-thirds of the tongue, to the parotid gland and guttural pouch, to the integument covering the lower half of the head, and to the muscles of mastication. In addition, the *lingual fibres* not only supply sensation to the tongue, but are distributed to the fungiform papillæ, and so assist in the sense of taste.

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* 'Veterinary Anatomy.'

† Sisson, *op. cit.*

‡ Sisson, *op. cit.*

If the fifth pair of nerves be divided, there is complete loss of sensation to one half of the face, part of the ear, cornea, conjunctiva, nasal mucous membrane, and anterior two-thirds of the tongue. There is paralysis of the muscles of mastication, the mouth and tongue become injured by the teeth, in consequence of the loss of sensation; the food collects on the paralysed side of the mouth; the cornea ulcerates, either in consequence of the loss of trophic influence, or, as most physiologists think, from irritation caused by foreign bodies, of which the animal has no knowledge, in consequence of sensation being lost. Division of the superior maxillary branch in the horse—known as **Bell's experiment**—prevents the animal from feeding, owing to inability to grasp the food with its lips. Now, as this is a sensory and not a motor nerve, the question arises, Why is the animal prevented from grasping its food? It is the duty of the sensory branches of the fifth to keep the muscles informed of the position of objects. When sensation is cut off, owing to the entire loss of sensibility in the lips, the animal cannot know how to take hold of the food. It can see the material in the manger, but, in consequence of loss of sensation, does not know how to employ the muscles of the lips to collect it.

There are certain reflex acts in which the sensory branches of the fifth are intimately concerned. When sensation is cut off, the 'feelers' growing from the orbit are unable to excite the reflex act of closing the eye. Irritation of the Schneiderian membrane produces no sneezing, and irritation of the conjunctiva or of the cornea does not produce tears, while the loss of sensation in the tongue means failure in the stimulus for the secretion of saliva.

Ninth Pair, or Glosso-pharyngeal.—This nerve, consisting of a motor and a sensory portion, arises by several roots from the anterior and lateral part of the bulb. As it leaves the cranium, a ganglion is found on it—the *ganglion petrosum.* This ganglion is connected with the superior cervical ganglion of the sympathetic and the jugular ganglion of the vagus. There are three branches of nerves distributed from the petrous ganglion: one passes to the *cavity of the tympanum,* and supplies sensory branches to the mucous membrane of the tympanum; a second is a motor nerve, and supplies the *muscles of the pharynx;* while the third branch is sensory, and supplies the posterior third of the *mucous membrane of the tongue,* part of the pharynx, and anterior face of the epiglottis. In this branch are taste fibres, which end in the 'taste bulbs' of the circumvallate papillæ.

Tenth Pair, Pneumogastric or Vagus.—This is a mixed nerve, containing motor, sensory, and secretory fibres. There is no other nerve possessing such a wide distribution, for its fibres extend from the bulb to the anterior mesenteric ganglion in the abdominal cavity.

The nerve arises from the floor of the fourth ventricle and the nucleus of the solitary tract; its motor fibres are derived from the spinal accessory. Leaving the bulb, it passes through the *foramen lacerum,* and here the sensory root has a ganglion on it, the *jugular ganglion.* In conjunction with the spinal accessory, the vagus courses its way on to the guttural pouch; here the two nerves separate. The vagus now joins with the cervical sympathetic, from which results, in the horse and most other animals, a single cord, which passes down the neck in company with the carotid artery. As it enters the chest, the vagus separates from the sympathetic, and the right and left trunks proceed on their way. They both give off important branches, known as the 'recurrent laryngeals,' fibres to the heart, trachea, bronchi, and œsophagus, and then each divides into two branches, dorsal and ventral, which come together from opposite sides and form the dorsal and ventral œsophageal branches. These penetrate the diaphragm, after running above and below the œsophagus. The dorsal branch, composed mainly of fibres from the right vagus, passes to the cardia of the stomach, gives off many fibres to that organ, and, continuing its course backwards, joins the anterior mesenteric ganglion (solar plexus) of the sympathetic (Fig. 81). The ventral branch of the œsophageal nerve proceeds to the lesser curvature of the stomach, while fibres pass on to the duodenum and liver. In this way the vagus supplies fibres to the larynx, trachea, bronchi, lungs, heart, œsophagus, stomach, duodenum, liver, and through the sympathetic ganglion fibres to the small and to a portion of the large intestines. In the chapters dealing with the heart, circulation, respiration, and digestion, the special functions of this nerve have received full consideration. Nevertheless, there are some features of the vagus which may be conveniently dealt with here.

Through the jugular ganglion the vagus is brought into relation with the facial, glosso-pharyngeal, and spinal accessory nerves, and it is intimately connected in the neck, thorax, and abdominal cavity, with the sympathetic system (see p. 234). In the neck it gives off a *pharyngeal branch*, which forms a plexus with the pharyngeal branch of the ninth pair; and from this plexus motor fibres proceed to the middle and posterior constrictor muscles of the pharynx, and finally distribute themselves on the cervical portion of the œsophagus, to which they furnish motor power. The vagus next gives off the *superior laryngeal*, a mixed nerve, which supplies acute sensation to the mucous membrane of the epiglottis and larynx, and inhibitory fibres to the respiratory centre. It is this nerve which is reflexly excited in the act of coughing, and is capable of arresting inspiration, a very necessary provision at the moment of swallowing. The motor fibres in this nerve are the *external laryngeal*, given off before the main trunk enters the larynx, and supplying motor power to the crico-pharyngeus, crico-thyroid muscles, and in part to the œsophagus. Anatomists are not agreed as to the innervation of the crico-thyroid muscle in the horse. Moeller regards its motor supply as being derived from the first cervical pair; Chauveau and others, and recently Sisson, described it as being innervated by the external laryngeal nerve. The function of the crico-thyroid muscle being to render the vocal cords tense, division of the nerve produces a hoarse voice. Section of the superior laryngeal causes loss of sensibility in the larynx, and allows food to enter it. The *inferior or recurrent laryngeal* nerves are given off from the vagus within the chest. The right comes first, being given off opposite the second rib, and winding around the dorso-cervical artery from without inwards, while the left is given off above the base of the heart, the nerve winding from without inwards around the posterior aorta. Both nerves leave the thoracic cavity and return up the neck. This complicated arrangement resembles very closely the ' out-of-the-way ' course taken by the spinal accessory in order to reach the trapezius. From the points where each recurrent is given off within the chest their courses are not identical; the left, for instance, having a greater distance to travel, is somewhat mixed up with the structures around the base of the heart, while in its passage up the neck it is more superficially placed than the right recurrent. Both nerves supply motor power to all the muscles of the larynx, with the exception of the crico-thyroid. All the fibres in the recurrents are not motor; in their passage up the neck sensory branches are given off to the trachea and œsophagus. At p. 152 sufficient consideration has been devoted to the subject of paralysis of the laryngeal muscles and its influence on respiration. The question is of intense practical interest, owing to the frequency with which the innervation of these muscles is destroyed on the left side. At present there is no satisfactory explanation of this unilateral paralysis. After division of both recurrent nerves, both sides of the larynx are paralysed, and in horses asphyxia is gradually produced. The writer has, however, seen bilateral paralysis not seriously interfering with slow work. In such cases it is believed that the age of the horse is the saving factor; the cartilages, becoming rigid with age, prevent the arytenoids from completely collapsing over the opening of the glottis. If the recurrent nerve on either side of the neck be divided and the horse galloped after the operation, he is found to be a 'roarer.' Not only does paralysis of these muscles interfere with respiration, but it also affects the voice. The altered character of the voice of the horse may be observed either during neighing or coughing. So distinctive, indeed, is the cough of a 'roarer,' that such cases may be at once recognised. Longet found that dividing the recurrent led to loss of voice in old animals, while in the young the voice was rendered unnatural and shrill. This shrill condition was entirely lost by cutting the external laryngeal, which, by paralysing the crico-thyroid, prevented the vocal cord from being stretched, and so rendered the animal mute. If the peripheral end of a divided recurrent be stimulated, spasm of the larynx is produced. There are certain vegetable poisons, such as those contained in *Lathyrus sativus*, and other plants of the Leguminosæ, which appear especially to single out this nerve. Horses fed on grain containing *Lathyrus* are soon rendered incapable of work, as asphyxia occurs through spasm of the larynx.

Chauveau, in his experimental inquiry on the vagus of the horse, found that if both vagi be divided in the neck and the animal fed, the stomach and whole length of the œsophagus frequently became greatly distended with food, in consequence of loss of motor power. It seems certain that the sensation of repletion in these cases is lost; this conjecture would account for the animal continuing to eat.

SECTION 8.

The Sympathetic or Autonomic System.

The function of the system of nerves derived from the spinal cord, with which we have hitherto dealt, is connected with the movements of the skeletal muscles and the question of sensation; but there are other highly important matters which need nervous control and yet are not within the knowledge of the animal. To the old physiologists these were known as the ‘vegetative’ functions, presided over by a system of nerves described as the sympathetic, which was believed to be independent of the cerebro-spinal. These vegetative functions comprised the movements of the heart, bloodvessels, and abdominal viscera. The work of Gaskell and Langley has altered the entire conception of the sympathetic system, and even changed its name; it is now known as the **autonomic.** The nerve-centres in the brain and spinal cord are enclosed within a bony framework; contrarily, the nerve-centres in the sympathetic system are lodged in various tissues and organs of the body, outside and at varying distances from the cranium and spinal canal. The old conception of the sympathetic system was that of a cord of nervous matter which extended from the base of the skull to about the first bone of the tail, and on which were situated certain nodules of nervous matter known as ganglia; from these ganglia plexuses of nerves arose to supply the heart and bloodvessels; connected with this long cord were other ganglia situated in the abdominal cavity, the plexuses of nerves from which supplied the abdominal and pelvic viscera. There is nothing in the modern conception which conflicts with this account of the anatomical arrangement, but there is a great deal which amplifies and extends the former description. It is now known that it is not a system independent of the brain and spinal cord, but that it is intimately connected with both, and obtains from each the nerve-fibres with which it works. Through the activity of the various ganglia it possesses it elaborates these fibres into a system peculiar to its own requirements, and then proceeds on the lines of self-government to carry out its functions without any further reference to the brain or spinal cord. It thus possesses an abundant supply of efferent nerves derived from the brain, but especially the spinal cord; in return, however, it gives little, for afferent nerves are few and far between, and, moreover, their sensibility is blunted.

The structure of the fibres in the sympathetic system is much the same as in the cerebro-spinal; the fibres are white or grey, but principally grey, and in point of size they are much finer. Similarly, the ganglia do not differ in structure from the nerve-centres found in the cord; they contain multipolar cells. It was the presence of these multipolar cells which at one time led to the belief that the ganglia of the sympathetic system were centres of reflex action, but there are no definite reflex actions in this system of nerves, although it works as a reflex effect—that is to say, not under the control of the will. Nevertheless, there are some well-known facts which suggest that sympathetic ganglia may initiate reflex action; the most obvious example of this is the peristaltic movements of the intestines when removed from the body, and after all nervous connections with the spinal cord have been severed.

Construction of the Autonomic System.—The way in which the old sympathetic system of the anatomists is linked up with the cerebro-spinal system to form the autonomic system of nerves must now be explained. The linkage with the brain is furnished by the third, seventh, ninth, tenth, and eleventh pair of cranial nerves. On the sympathetic trunk in the neck are two, sometimes three, ganglia—namely, the superior and inferior cervical, and in the horse occasionally a middle cervical. The superior cervical ganglion is connected with the last four cranial nerves and with the first cervical from the spinal cord; the inferior cervical ganglion is connected with the sixth and seventh cervical nerves and through a band of nerves accompanying the vertebral artery it is also linked up with the spinal cord from the second to the sixth cervical nerves. The arrangement in the remaining portion of the spinal cord is different: the sympathetic trunk leaves the inferior cervical ganglion and gains the ribs close to the heads of these; here it may be distinctly seen beneath the pleura, and at each intercostal space it possesses a nodule or ganglion. Throughout the length of the dorsal, lumbar, and sacral vertebræ this cord runs, and throughout its length it is brought into close linkage with the spinal cord in the following way:

With the ventral roots of the spinal nerves there pass out of the canal white medullated fibres, known as the *white rami*, which leave the ventral root and run to the ganglia on the sympathetic cord; these ganglia are known as the *vertebral*. Many of the white rami connect with the vertebral ganglia and issue from them generally as grey fibres, known as *grey rami*, which then rejoin the ventral roots of the spinal nerves and proceed to their destination in the mixed nerves (see Fig. 163). When the fibre enters the ganglion as a white ramus, or *preganglionic fibre*, its axon breaks up and arborises around the dendrites of a sympathetic cell; it then reissues, as we have stated, as a grey ramus, or *post-ganglionic fibre*. Not all the white rami terminate in the vertebral ganglia; some having reached this point pass through, and proceed to other and more distant ganglia of the sympathetic—for example, the mesenterics and the semilunar, which form the system designated the *collateral* or *prevertebral ganglia*. The nerves intended for these enter as white rami, arborise around the cells, and emerge as grey or postganglionic fibres, and proceed to their destination; those intended for still more distant ganglia, such as those of the intestines, do not arborise in, but pass through the collateral ganglia still as white rami or preganglionic fibres, and so reach their destination, the *terminal* ganglia, there finding their cell-stations (see Figs. 163, 164).

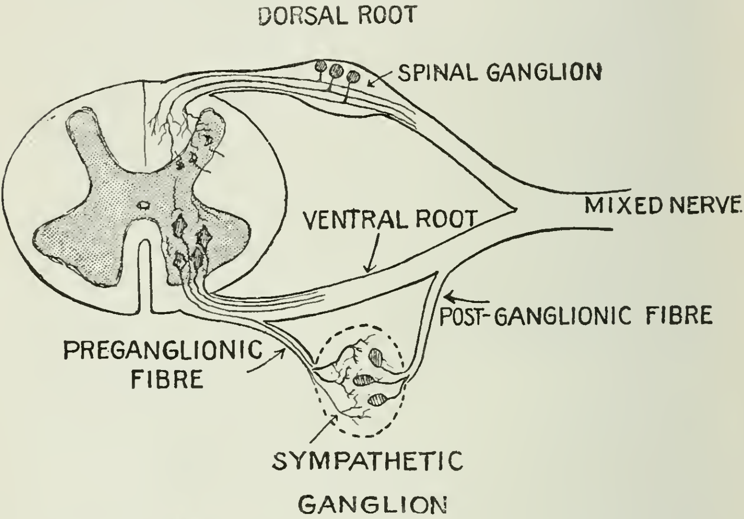

Fig. 163.—Diagram showing the Arrangement of the Dorsal and Ventral Roots of the Cord and the Connection of the White and Grey Rami with the Ventral Root.

The sensory fibres are shown passing through the spinal ganglion and entering the cord through the dorsal root. The motor fibres leave the cord by the ventral root. Shortly after leaving the white ramus is given off, shown in the diagram as the *preganglionic fibre*. This passes to a lateral (vertebral) ganglion of the sympathetic system, makes a cell connection as shown in the diagram, and issues as a *grey ramus*, or *post-ganglionic fibre*, which rejoins the ventral root.

The cell-stations, then, for a preganglionic fibre must be a vertebral (or lateral) ganglion, a collateral (or prevertebral) ganglion, or a terminal ganglion. An immense amount of work has been done by Langley and his fellow-workers in determining the cell-stations of the whole system of spinal linkage with the sympathetic system. Langley found that *nicotine* applied to the ganglion had the effect of paralysing the nerve-cells, but not the nerve-fibres. In order to ascertain whether a nerve-fibre had its cell-station in any given ganglion, the ganglion was painted with nicotine, and if the nerve on stimulation continued to function it was evident that it made no cell connection.

Every preganglionic fibre must have its origin in the midbrain, bulb, or cord, so that every autonomic fibre consists of two neurones, the first lying between the cell of origin and the sympathetic ganglion in which it terminates, the second neurone being placed between the ganglion in which it terminated and the tissue supplied. In other words, the preganglionic and post-ganglionic fibres represent the two neurones in the autonomic chain; to this there is no exception; it is a fundamental principle in the construction of this peculiar system. It is not necessary that a preganglionic fibre on its way to join a vertebral ganglion should pass to that which is nearest to it; it may pass forwards or backwards among the vertebral ganglia until it finds the one in which its cell-station exists. In consequence, a post-ganglionic fibre derived from a vertebral ganglion does not always rejoin the spinal nerve with which it left the cord, while the post-ganglionic fibres derived from the prevertebral or terminal ganglia never return to the spinal nerve.

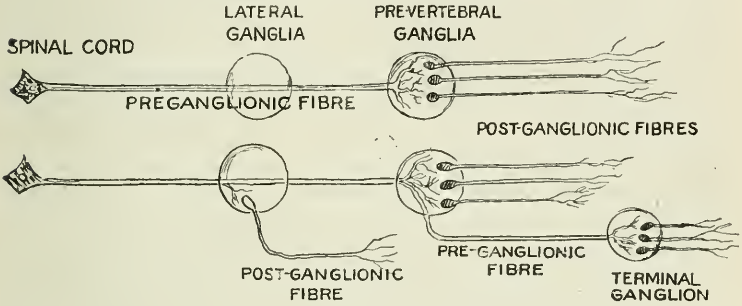

FIG. 164.—DIAGRAM OF THE AUTONOMIC GANGLIA.

The preganglionic fibres issue from the spinal cord, and in the upper figure are shown as passing through, but forming no cell connection with, the lateral (vertebral) ganglion. As a preganglionic fibre it continues, and makes a cell connection in the next, or prevertebral ganglion, from which the post-ganglionic fibres issue.

In the lower figure some of the preganglionic fibres have formed a cell connection with the lateral ganglion, and issue as post-ganglionic fibres. Others pass through, still as preganglionic, and some of these form cell connections in the prevertebral ganglion; others do not, and, continuing as preganglionic fibres, reach the terminal ganglion, where they arborise; from this post-ganglionic fibres issue.

Post-ganglionic fibres are more numerous than preganglionic; this is effected by the nerve arborising around several cells in a ganglion, from each of which a fresh neurone issues; by this means considerable economy of space is effected in the spinal canal.

Functions of the Autonomic System.—The function of this curious system of nerves is to govern the movements of the heart, viscera, bloodvessels—in fact, of all involuntary muscles—and to bring about the various secretions; it regulates those functions over which no voluntary control can be exercised.

Very little reflection will show that the autonomic system cannot be confined solely to nerves derived from the spinal cord. In the head are bloodvessels and involuntary muscles, such as the iris, which require 'innervation,' and glands which are called upon to secrete. These tissues are supplied by cranial and not by spinal nerves. Evidently, then, some cranial nerves function as autonomic, and no better example of this can be given than the pneumogastric. The autonomic system consists, therefore, of a cranial and a spinal system.

The Cranial Autonomic System.—The ciliary ganglion on the third pair of nerves furnishes post-ganglionic fibres to the involuntary muscle of the iris and ciliary muscle. The seventh pair furnishes the chorda tympani so intimately concerned in the secretion of saliva, while fibres from the seventh and ninth pair supply dilator fibres for the bloodvessels of the mouth, nasal chambers, and salivary glands, through various ganglia, such as the otic, submaxillary, and sublingual. The tenth and eleventh pair have abundant autonomic fibres which furnish viscero-motor fibres to the œsophagus, stomach, small, and part of the large, intestines (see p. 235), motor fibres to the involuntary muscle of the bronchi, inhibitory fibres to the heart, secretory fibres to the gastric glands and pancreas, and nerves to the liver, spleen, and kidneys. The cell-stations of these are not known with precision; most of them are probably located in the tissues supplied.

The **Spinal Autonomic System** is far better known, and consists of vasomotor nerves, dilator and constrictor, secretory nerves for the skin and viscera, erector fibres for the hair, and viscero-motor nerves, both excitatory and inhibitory. Throughout the dorsal, and part of the lumbar, area vasomotor (chiefly constrictor), sweat, and pilo-motor fibres are abundant—especially the vasomotor. Those having their cell-stations in the vertebral ganglia are intended to supply the skin of the trunk and limbs; the fibres for the skin of the head and neck do not terminate in the vertebral ganglia, but join the cervical sympathetic, and issue as post-ganglionic fibres from the superior cervical ganglion. The vasomotor, especially constrictor fibres for the abdominal viscera, do not return to the spinal mixed nerves for distribution, but proceed, mainly in the splanchnic nerves, to the solar and mesenteric ganglia, and issue from these as post-ganglionic fibres. The splanchnic nerves are the great vaso-constrictor nerves of the abdominal cavity—in fact, the largest constrictor nerves in the body, also the viscero-motor, both excitatory and inhibitory, of the intestinal wall.

From the sacral cord the autonomic fibres in the ventral roots pass out without making connection with the vertebral ganglia, and proceed as the *nervus erigens* to the pelvic plexus. They supply the external organs of generation with vaso-dilator fibres, the single colon and rectum with viscero-motor. The vaso-constrictor nerves for these parts are derived from the dorsal and lumbar cord, reaching their destination via the sympathetic by means of the hypogastric nerve or the pudic nerve. The bladder receives two sources of viscero-motor supply, which has been described (p. 355).

It will be seen that through the autonomic system of nerves impulses of an opposite nature pass to the various tissues—for instance, to the bloodvessels, mainly constrictor, but also dilator effects, to the visceral muscle contractile or inhibitory impulses. The same branch of nerve, though not the same fibre, may be conveying vasomotor and viscero-motor impulses of an opposite type, so that, as in the case of the heart, there are nerves which are bringing about increased activity, *katabolic*, and inhibitory nerves effecting repair, *anabolic*. While the cell-stations for the katabolic nerves are generally in the vertebral or else the prevertebral ganglia, those of the anabolic nerves are generally in the prevertebral or else the terminal ganglia.

Activation of the Sympathetic System.—The sympathetic muscular system is activated by the ordinary nervous impulse and by the secretion of the adrenal bodies; one acts by direct contact with the plain muscle, the other operates from a distance. At p. 304 it was stated that the medulla of these endocrine glands was a portion of the sympathetic system, and that they poured their secretion, *adrenaline*, into the blood-stream. Adrenaline cells and sympathetic ganglion cells are brother and sister (T. R. Elliot). Constriction of the bloodvessels and secretory activity are maintained by adrenaline, while the rate and rhythm of the heart's action are stimulated by its influence on the sympathetic nerve-endings in that organ. The effect of adrenaline on the sympathetic system is obliterated by the action of a substance obtained from ergot, known as ergotoxine or acetylcholine.

Sensory Phenomena in the Autonomic System.—It has already been stated that the majority of fibres in the sympathetic system are efferent; afferent fibres are known to exist, but there is very little information concerning them. As a rule, the parts supplied by the sympathetic system are devoid of ordinary sensibility; the existence, therefore, of afferent fibres must be very limited. The intestines can be handled, burned, cut, or sutured without the animal evincing pain; the heart can be injured in many ways without giving any sign of sensibility; the liver, spleen, and kidneys are equally devoid of touch sensibility, and are ordinarily free from painful impressions.

It is no wonder that to the majority of people the interior of the body is non-existent as a sensitive area. Notwithstanding the normal insensibility of the part, the most acute pain experienced by the horse is referred to the abdominal cavity. There is no pain to equal that caused by a twisted condition of the intestine, and an attack of acute colic comes next in order of intensity The explanation lies in the fact that the parietal peritoneum is extremely sensitive, and that the mesentery with its attachments when dragged upon produces acute pain. Nor is tension as a cause of pain confined to the mesentery; great distension of the hollow viscera causes acute suffering, as also may any irritation within the hollow viscera; the passage of a gall-stone in man is attended with intense pain, due to the stretching of the duct. This class of pain is not referred to the viscera, but to the abdominal wall, and the explanation which has been offered is that the sensory cutaneous nerves belong to the segment of cord in which the afferent nerves from the viscera end, and the pain is thus referred to the skin; it is known as *referred pain*.

Nevertheless, Flourens observed that the sympathetic ganglia were sensory in different degrees, but always less so than the nerves of the cerebro-spinal system. He frequently noticed that stimulation of the semilunar ganglion of the rabbit caused acute pain, while stimulation of the cervical ganglion was unnoticed. Many observers following Flourens record the same fact regarding the sensory character of the semilunar ganglion when stimulated. Colin, in his observation on the degree of sensibility of the sympathetic ganglia in horses, oxen, dogs, and rabbits, agreed with Flourens that these tissues were endowed with different degrees of sensation, and that the semilunar and thoracic were more sensitive than the upper cervical. He found that the rapidity with which a painful reaction showed itself depended on the strength of the stimulus, weak stimuli taking several seconds before any evidence of pain was given. He also found that if the gastric, splenic, hepatic, and intestinal arteries were pinched with forceps, stretched, or damaged, great pain was shown. These facts, perhaps, enable the pain of colic, and especially of intestinal twists, to be explained, though why horses can carry in their intestines stones, sand, gravel, and calculi, week after week and month after month, without pain being produced is still unknown.

Pathological.

The absence of alcoholism and syphilis in the lower animals reduces the incidence of nervous affections. It cannot truly be said that worry or anxiety are absent among them, and that hence nervous affections are not so frequent. Nervousness is characteristic of all horses, while to realise that anxiety cannot be denied to the lower creation, one has only to witness what occurs when their young are taken from them.

We have seen that the brain is relatively lowly organised in the inferior animals, while the cord is relatively highly organised. Brain trouble is consequently not so frequent as disorders of the cord.

In the horse the old class of disorders known as **megrims** and **staggers,** with its varieties of *sleepy* and *mad*, are now rarely described, and probably as rarely seen. They appear in the main to have been due to two causes—dietetic errors and the obliteration, more or less complete, of the jugular veins as the result of ' bleeding.' We still meet with *ship staggers* in bad weather at sea, the result, apparently, of the horse's inability to vomit. The condition would appear to be produced by some reflex effect through the vagus. Another reflex nervous affection is *hysteria.* **Abscess** of the brain may result from septic infection, especially that of *strangles*. **Tumours** of the choroid plexus are not uncommon in the horse; they are composed of cholesterine. **Hydatids** in the substance of the brain of sheep and cattle are well known. True inflammation of the brain and its coverings is probably unknown in the herbivora, excepting as the result of surgical conditions or of the virus of **rabies.**

Paralysis of the hind-quarters, partial or complete, is common, and a variety of disorders are probably concerned, quite apart from those due to injury. Paralysis in the horse is common in India, and some cases may be associated with parasitic invasion; in temperate climates, noxious substances in the food are recognised as a cause. In *azoturia*, *venereal disease of equines*, and *embolism* of the iliac arteries it occurs as a symptom. *Enzootic paralysis* is frequently recorded in connection with feeding on certain kinds of grass and hay, while other nervous affections exist as epizootics of sheep; **louping ill** has been traced to infection by a specific microbe. Of the local paralysis known as **roaring** sufficient has already been said at pp. 152, 156. Local paralysis in the fore-leg may also occur as a result of a fracture of the first rib. The fact, however, remains that we know little or nothing of the nervous diseases of animals; take, for example, **shivering** and **springhalt,*** spasmodic affections, the latter characterised by more or less violent flexion of a hind-limb, due to the unbalanced action of the flexor muscles. The cause of one spasmodic disease, **tetanus,** is clearly known, but the others are still wrapped in obscurity.

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* Vulgarly known as *stringhalt,* a meaningless expression, a degeneration of the word springhalt accurately employed by Shakespeare (' Henry VIII.,' I. iii. 11-13).

CHAPTER XV

THE SENSES

Section I.

Sight.*

Light.—The energy which produces light is transmitted from the sun to the earth by means of wave motions in the ether; the wave motion is produced by oscillations of the ether in all directions at right angles to the line of propagation of the energy. The velocity of the ether waves is 186,000 miles a second, but their rate of oscillation varies. Some are relatively slow, and are not perceived as light, but as heat; still slower oscillations (from 3,000,000 to 15,000 per second) are characteristic of waves used in wireless telegraphy. On the other hand, there are oscillations of incredible velocity, some of which produce X rays, others ultra-violet rays, and others, of slower movement, visible violet rays; the last are produced by oscillations in the ether of 1,200 billions per second; red light has only half this number of oscillations. The rate of oscillation determines the length of the wave; the more rapid the oscillation, the shorter the wave length; a wave length is the distance from crest to crest.

Ordinary light consists of a mixture of red, orange, yellow, green, blue, and violet lights. When brought together, these colours form white light, and when white light is passed through a prism it is decomposed into its primary colours (see Fig. 165). A beam of sunlight entering a prism becomes bent or *refracted ;* the various rays are unequally refracted, the red being the least, the violet the most bent. There are rays beyond the red and the violet which are invisible to our eyes; they are known as the ultra-red (heat rays) and ultra-violet (chemical rays). Every lense disperses light in the same way as a prism, and both in the eye and in every optical instrument dispersion is corrected.

The **Eyeball,** surrounded by a protective layer of fat, is placed in a socket partly of bone and partly fibrous which, together with the muscles, affords the bulb and optic nerve complete protection. A very severe blow is required to break the bony rim, but the transparent, refractive part of the eye is necessarily exposed and is readily injured. The size of the orbital rim is such that infinitely more harm may be inflicted on the eye by small than by large bodies. The external tissues of the eye are dense and resisting, but the internal structures are delicate and readily displaced from their position.

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* In the revision of this section many points have arisen necessitating observations on the living animal for which the writer has no facilities. He is accordingly greatly indebted to Captains Minett and Oxspring, of the Army Veterinary School, Aldershot; Professors Linton and Mitchell, of the Royal (Dick) Veterinary College; and Messrs. H. Gray and J. B. Robertson, M.R.C.V.S., for several observations.

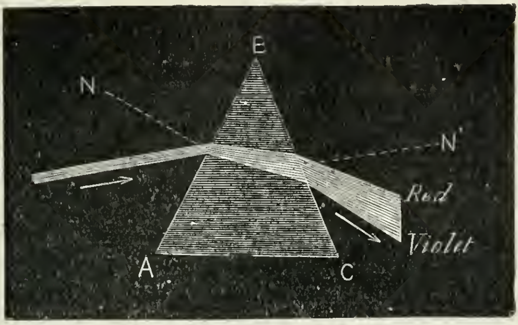

FIG. 165.—REFRACTION AND DISPERSION BY A PRISM (STEWART).

The beam of light is bent towards the normal N as it passes across B, A, and away from the normal N′ as it passes across A, C. At both surfaces it is bent towards the base of the prism A, C. At the same time the light suffers dispersion—that is, the rays of shorter wave-length are more refracted than those of greater wave-length. This splits up light into its constituent colours.

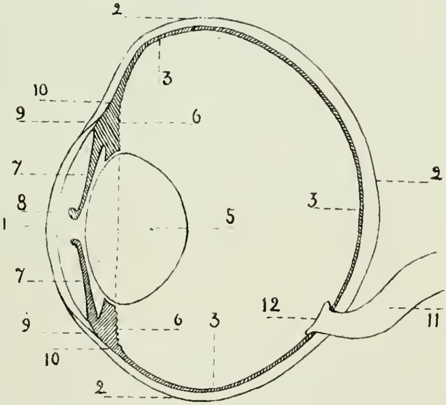

FIG. 166.—SECTION OF THE EYEBALL OF THE HORSE.

1, The cornea; 2, sclerotic; 3, choroid; 5, the lens (the dotted line around the equator indicates the position of the suspensory ligament of the lens); 6, ciliary processes; 7, the iris; 8, corpus nigrum; 9, corneo-scleral junction; 10, ciliary body (where the dotted line terminates is the position of the narrow ciliary muscle); 11, the optic nerve with its 'kink' penetrating the sclerotic very low down; 12, the optic disc.

The eye as an optical instrument is not perfect. It has been stated above that there are certain rays beyond the red and violet which it cannot see, and, furthermore, there are frequently defects in its refraction, more or less considerable, which prevent the formation of a clear picture. The principle of its construction is that the rays of light enter through its transparent anterior coat, then pass through a fluid medium of greater refractive index than the air, then through a lens, next through a fluid, glass-like substance, and finally reach a nervous expansion at the back of the eye, where the picture is formed. There are also present mechanisms for limiting the amount of light entering the eye, and for bringing the rays of light to a correct focus. The familiar instrument known as the camera is a very close reproduction of the eye. It possesses its lense for refracting the rays, its diaphragm for limiting the number admitted, its sensitive plate for receiving them, and its focussing arrangement for producing a sharp image. The various structures of the eye and its accessories will now be looked at for their physiological importance, the eye of the horse being taken as the standard.*

The **Eyelids** are remarkable for the fineness of the skin entering into their structure, for the absence of fat, and the mobility of the upper as compared with the lower lid. The surface next the eyeball is lined by the conjunctiva. The slit formed by the union of the two lids is longer than the cornea, so that a portion of the sclerotic may be seen; ordinarily, since the conjunctival membrane covering it is pigmented, the white sclerotic is not obvious, excepting the palpebral fissure be widely dilated, or the part be depigmented. The size of the fissure during repose is sufficient to expose the greater part of the cornea, but during excitement or anger it is much deeper, and the whole cornea is completely exposed. The eyelids lie in close approximation to the eyeball, especially the lower. This approximation of the lower lid is essential for the drainage of the conjunctival sac; otherwise the tears would run over the face. The lids are given firmness by the presence in them of a tarsal cartilage; along the edge is situated a rim of glands which secrete a somewhat unctuous material which assists to prevent the tears from running over the face. The eyelids are closed by the orbicularis muscle, which mainly operates on the upper lid; its antagonist arises far back within the orbit and runs to the upper lid; the shape of the eyeball alters the direction of the pull of the levator. When the eyeball is removed the upper lid can no longer be raised.

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* For a detailed account of the comparative anatomy of the eye, see 'Veterinary and Comparative Ophthalmology,' by Dr. E. Nicolas, edited and enlarged by H. Gray, M.R.C.V.S., 1914.

Excepting by a distinct effort, the palpebral fissure is never entirely closed in the horse, even during sleep; the lid droops over the cornea, so that it may be said the animal sleeps with his eyes open. If he is lying down, the lowermost eye is closed. The dog and cat sleep with both eyes closed; the sheep and ox behave much as does the horse.

The **Eyelashes** on the lower lid are few and very fine, while on the mid-region of the upper lid they are abundant, long, and strong, and exist as a double row, the rows crossing each other trellis-wise, but without interlacing (Fig. 167). A few long protective hairs grow from the brow and below the lower eyelid; they may be as much as 4 or 5 inches in length in some horses.

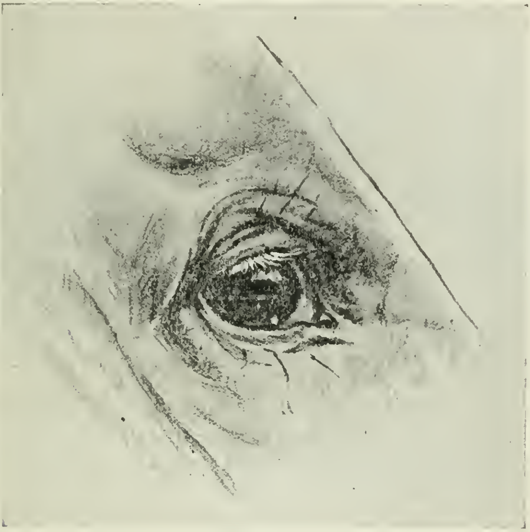

FIG. 167.—THE EYE OF THE HORSE.

They are connected with special nerve terminations, and the delicacy of their sense of touch is remarkable. This function is protective; they give the eyes warning of danger.

The **Membrana Nictitans**, or third eyelid, is functionally active in all animals below man and the monkey, though not to the same degree in each. Least active in the cat, owing to the use made of the fore-limbs, it is seen in its highest development in the horse, boldly and rapidly sweeping across the globe of the eye when required, and when out of action lying almost unobserved away from the line of sight on the inner aspect of the eyeball. Its basis is a curved piece of cartilage, thin on that edge which can be seen lying next to the globe of the eye, but thick and embedded in fat at its deep part within the orbit. The movement of the membrana is brought about indirectly; the retractor muscle pulls the globe of the eye well within the socket, which causes a forward displacement of the fatty cushion connected with the cartilage. The cartilage is naturally curved, but becomes flattened and straightened out by the pressure caused by the retractor, and in consequence is shot forward; when the retractor relaxes the eyeball comes forward, the pad of fat recedes, and the cartilage retires, taking up its curvature through its own elasticity. The earliest symptom of tetanus in the horse is a protrusion of the membrana nictitans, the result of spasm of the retractor muscle. In connection with the *membrana* is found a gland resembling the lachrymal; it is known as the *gland of Harder*, and is developed to a remarkable degree in the ox.

The Lachrymal Apparatus.—The lachrymal gland lies under the orbital process; in the ox it is very large. Its ducts, of which there are several, open into the conjunctival sac high up under the upper lid. The lachrymal fluid for the lower lid is obtained by gravity. The fluid is conveyed from the eye by means of a duct which has two openings, one on the upper and another on the lower eyelid, the lower being the larger. The fluid is directed into the slit-like openings of the duct by means of the *lachrymal caruncle*. The ducts enter the *lachrymal sac*, which communicates with a canal that finally opens into the nasal chamber by a passage which is sometimes duplicated in the horse, and is relatively large.

The function of the lachrymal secretion is to preserve the brilliancy of the surface of the cornea, and to flush the lachrymal sac when this is occupied by an irritant. Man is said to be the only animal capable of weeping, but H. Gray has seen it in the cat, and it is recorded as occurring in the elephant and seal. A few tears may run down the cheek of the horse when the cord is divided behind the medulla, but tears are never seen during life.

The Orbit.—The entire contents of the orbit—viz., eyeball, muscles, gland, nerves, vessels, and fat—are enclosed in a fibrous, funnel-shaped membrane which posteriorly obtains attachment where the optic nerve issues from the skull, and in front is attached to the orbital rim. The sheath is held in position by several bands. The structures are thus not only protected by, but confined within, a membranous case; the interval between the sheath and the eye-socket is filled with fat, which acts as a cushion. There is fat within this sheath also, the largest mass being on the inner side of the eyeball. The use of this pad of fat, in pushing forward the membrana nictitans when the retractor muscle contracts has already been mentioned.

The **Muscles of the Eyeball** are seven in number—four *recti*, two *oblique*, and one *retractor*. The use of the recti is to rotate the eyeball upwards, downwards, inwards, and outwards. All the recti muscles are attached squarely to the sclerotic at slightly varying distances from the cornea; the nearest to the cornea is the external rectus; judging by its weight, it is a stronger muscle than the internal rectus. These four muscles would be capable of doing all that was required in the matter of movement were it not that the visual axis of the eye must always be kept parallel to the horizon, and this the recti muscles cannot accomplish for the reason that the position of the visual field of the eye has to be adjusted to the movements of the animal's head. No matter what position this occupies, whether it be depressed, as in grazing, or elevated by the muzzle being pressed upwards, the pupil remains practically horizontal. This peculiarity can be especially well studied in animals with a horizontal pupil, which acts like a spirit level, and demonstrates unmistakably the wheel-like rotation of the eye (Fig. 168). When the head is in the normal position the pupil is horizontal; if there was no torsion of the eyeball the nasal side of the pupil during grazing would be placed obliquely downwards, and in the elevated head obliquely upwards—almost vertical, indeed, resembling that of the cat. The oblique muscles cause the globe of the eye to be twisted obliquely either upwards or downwards around its antero-posterior axis, in order to insure that the visual axis of the eye is always so presented to the outer world that the picture on the retina will be parallel to the horizon. When the superior oblique contracts it pulls the temporal side of

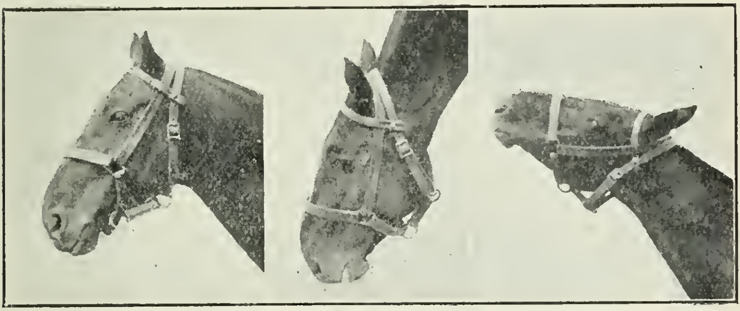

Fig. 168.—Various Positions of the Horse's Head relative to the Direction of the Pupil.

The pupils cannot be seen, but the alterations in the position of the orbits are well shown as the result of depressing or elevating the head.

the eyeball upwards, and if it were not antagonised by the inferior oblique, it would render the pupil almost vertical; the inferior oblique pulls the temporal side of the eyeball downwards. This wheel-like movement is regulated from the semicircular canals of the ear.

If the head be greatly elevated, the eyeball is depressed in the socket, the cornea partly disappears beneath the lower lid, and the sclerotic shows considerably above (see Fig. 168). This is part of the mechanism for keeping the visual axis of the eye parallel to the horizon, and is due to a conjugate action of the inferior rectus with the superior oblique.

It has been remarked that animals largely supplement eye movements by head movements, and this is true. The chief movements of the eyeballs are backwards and forwards, corresponding to outwards and inwards in man, and for this action the internal and external recti are responsible, but neither of these can maintain a horizontal pupil; they have accordingly to work in conjunction with the oblique muscles. In grazing, the superior rectus is of especial use by pulling the eyeball upwards, and so keeping the visual axis of the eye exposed to the horizon, while the oblique muscles keep it level. Animals do not require to look to the ground in grazing; though the face narrows below the eyes, it is impossible for them to see what they are eating; they are guided entirely by the sense of smell, their eyes being ' on guard.'

The anatomical arrangement of the oblique muscles enables them to carry out their function of maintaining a horizontal field of vision. The loop through which the superior passes before joining the eyeball alters the direction of the pull, while the inferior oblique has its origin remote from the recti and superior oblique, and is so placed as to act at right angles to the globe. Both muscles are worked from the nasal side of the orbit, but inserted into the *temporal* side of the globe, which arrangement affords a large range of movement.

The *retractor* muscle envelops the optic nerve and encircles the eyeball; it is inserted into the surface of the sclerotic behind the recti and oblique muscles. Its chief function is to withdraw the eyeball within the socket, and so work the membrana nictitans. By some it has been supposed to prevent the eyes projecting during grazing, but the recti could effect this; in fact, the recti acting simultaneously could retract the eyeball. It is not improbable that the retractor assists the recti, especially the inferior rectus. It is a voluminous muscle, and its lowest bundles run a long way forward beneath the eyeball. The antagonistic resistance to the backward pull of the recti and retractor muscles is said to be furnished by smooth muscle fibres in the palpebral portion of the capsule of Tenon; this capsule is inserted into the margin of the orbit as well as the upper lid.

Nerve Supply of Ocular Muscles.—No fewer than three pairs of cranial nerves are connected with the motor innervation of the seven muscles (p. 552). The *third pair* supplies all the muscles, with the exception of the external rectus and superior oblique, as well as the raiser of the upper lid. The *sixth pair* supplies the external rectus and part of the retractor. The superior oblique is innervated by the *fourth pair*, so that this one muscle has an exclusive cranial nerve-supply. The retractor muscle is supplied partly by the third and partly by the sixth pair. It is evident from what has been said that the muscles of the eyeball exhibit co-ordinate action; for example, if the sixth pair is acting on the external rectus, the fourth pair must also be in operation on the superior oblique, or else the pupil would not be horizontal. Similarly, if the internal rectus is contracting and a portion of the third pair thus functioning, the oblique muscles must also be in action to maintain the pupil horizontal. There is no movement of any of the recti muscles which is not associated with movement of the oblique muscles. When the movements of one eye are considered in relation to those of its fellow, the matter becomes more complex. Where the eyes are placed to the front it is evident that during the to-and-fro movements different muscles are being employed in either eye. If, for example, the eyes rotate to the right, the external rectus of the right eye is co-operating with the internal rectus of the left; such movements are called *conjugate*. Where the eyes are placed wide apart and situated towards the lateral sides of the face, as in the horse, the movements are not the same as in man; there is still, as with him in binocular vision, the outward and inward movements, better described as backward and forward, in which the muscles of the right and left eyes are conjugate, but there is, in addition, *binocular* vision, in which the movements of the eyes are in *opposite* directions, the right, for example, turned in to the left, and the left turned in to the right. This produces, so to speak, a double internal squint, and is the only position of the eyes in which the horse can see the same object with both of them at one and the same time. In this movement it is evident that the muscles of the eyeball are no longer conjugate, but *opposite ;* for the internal recti and the oblique muscles of both eyes contract simultaneously.

An interesting question here arises: When a horse is looking back at an object with one eye, does the opposite eye, which cannot see it, also look back ? The answer is in the negative. The movements of the two eyes are conjugate—*i.e.*, while the right is looking back, the left is looking forward. There are animals, however, capable of looking behind with both eyes, in which case the movement is opposite and not conjugate; this occurs in the hare and in birds.* The horse is also capable of seeing an object behind him with both eyes. The vision is very limited, for the animal invariably turns the head, if ever so slightly, in order to view the object with one eye and so obtain a larger visual field.

We can now turn to the globe of the eye, and consider its construction in special relation to its function.

The **Cornea** in most animals is circular, but in the horse and other domestic herbivora it is oval. If it be divided into two portions by a vertical line through the centre of the eye, it will be found larger on its nasal than on its temporal side. As a consequence of this, the curvatures of the cornea in the two meridians of the eye are not the same; the meridian in the horse, which is nearly always the flatter, is the horizontal. This excess of curvature of one meridian of the cornea over that of the meridian at right angles to it produces a defect in vision known as *astigmatism*. The cornea is a remarkably tough membrane, non-vascular, and richly supplied by nerves. It is nourished by lymph, which circulates freely through it. Glistening and transparent, it possesses in the horse a very narrow, opaque rim confined to the nasal and temporal portions of its circumference, where it is fitted into the sclerotic. The fitting is similar to that of a watch-glass into its case, for it thins out and runs under the sclerotic, which is here also thinned out. The conjunctiva of the eyeball ends at the rim of the cornea, and is here deeply pigmented. There are several layers to the cornea, one of them, the *membrane of Descemet*, being extraordinarily tough and quite vitreous in specimens hardened in formaline. The epithelium which lines the inner concave face is for the purpose of protecting the cornea against the watery fluid with which it is in contact—*i.e.*, the aqueous humour.

The cornea is one of the refracting surfaces of the eye; in man it is regarded as the principal refracting surface, but in the horse and dog the lens refracts more strongly than the cornea (Matthiessen). By reason of its prominence and of the great length of its horizontal meridian in herbivora, the cornea extends the field of vision, and so allows very oblique rays to be refracted. Johnson† points out that the cornea is large in all animals, having a divergence of more than 50 degrees to 60 degrees, and that in addition such animals have nearly spherical lenses, the spherical lense affording a wide angle of view.

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* W. Harris, M.D., 'Binocular and Stereoscopic Vision,' *Brain*, part cv., 1904.

† 'Comparative Anatomy of the Mammalian Eye,' G. L. Johnson, M.D., *Phil. Trans.*, vol. cxciv., B. 194, 1901.

The **Sclerotic** makes up the greater part of the surface of the eyeball. It is a dense, bluish-white, fibrous tunic; thickest behind, it thins at the equator, but is thinnest where its edge overlaps the cornea; it is also thicker on the temporal than on the nasal side, where it is protected from injury. It has a limited blood-supply, as might be supposed from its fibrous nature. It surrounds the globe of the eye to the extent of about four-fifths, and gives shape to the part. The eyeball is not a sphere in the herbivora; it is distinctly flattened posteriorly (Fig. 166), whereas in the carnivora it is more spherical. The cornea, which is let into its anterior face, is placed, not in the centre, but below the centre of the globe. This is especially marked in the horse (see Fig. 166). The length of the globe, measured from the cornea to the retina, averages in the horse 43·68 mm. (Nicolas and Gray); in the ox it is much shorter, 35·34 mm. being a mean, and the eyeball of this animal generally is much smaller than that of the horse. As a matter of fact, the antero-posterior diameter of the eye is liable to variation, which affects the refraction, as will be seen later. We have found the extreme measurements in the horse to be from 39·00 mm. to 42·75 mm. (1$\frac{3}{5}$ inches to 1$\frac{7}{10}$ inches).

The optic nerve, running in the substance of the retractor muscle, pierces the posterior wall of the sclerotic low down on its temporal side, after making a peculiar curve or dip (Fig. 166). This curve is necessitated by the horizontal movements of the eyeball; when the eye looks back the curve is increased, when it looks forward the ‘ slack ’ of the nerve is taken up and the curve entirely disappears.

The **Choroid** lies within the sclerotic. It may be regarded as the tunic which principally attends to the vascular supply; it furnishes an internal reflector to the retina by means of the *tapetum,* while its extension into the anterior region of the eye provides the iris, ciliary body, and ciliary processes.

The greater part of the choroid lies between the retina and sclerotic, enveloping and lining the whole of the vitreous or dark chamber as far forward as the ciliary processes. It consists of several layers: one, the vascular, for large vessels; a second, the capillary; and a third, the tapetum, which is the interesting physiological coat.

The **Tapetum Lucidum** is a peculiar, brilliant area of the posterior wall of the eye found in all domesticated animals but the pig. Its brilliant and beautiful iridescent colouring of yellow and bluish-green gives the appearance of pigment having been removed from the choroid.* The area of the tapetum is limited in size, being in the horse about 40 mm. in width and 25 mm. in depth, but there is a good deal of the tapetum still possessing its peculiar colouring, which is covered by dense retinal pigment, and therefore not exposed. The shape of the tapetum is roughly triangular, the base being just above the optic papilla. The tapetum is, therefore, in the optical axis of the eye. The colour in herbivora and carnivora, though not due to identical structural arrangement, is in both cases brought about by the decomposition of light, such as is diagrammatically shown in Fig. 165. In herbivora the decomposition is effected by the presence of a laminated fibrous structure; in carnivora by iridescent cells (Nicolas and Gray).

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* The pigmentary layer of the retina is always adherent *post-mortem* to the choroid, and for a long time was believed to be a choroidal tunic.

In whatever way the colour is caused, it produces a most beautiful object as viewed through the ophthalmoscope (Plate I., Fig. 4). Metallic and bluish-greens and yellow predominate in herbivora, yellow and orange in carnivora. There are no vessels in the tapetum; the surface in the horse is delicately stippled with brownish-green spots. The tapetum ends abruptly, there being almost a sharp line between the brilliant reflecting area and the dull brown retinal pigment of the surrounding choroid, a part which is sometimes spoken of as the *tapetum nigrum*. In albino and piebald horses the appearance of the tapetum is still more beautiful; there being no pigment, the whole of the back of the eye appears as a brilliant rainbow of colours in a pink setting. The appearance of the tapetum varies in different animals; that of the ox resembles the tapetum of the horse, but without the stippling; in the sheep the colour may be green or sky blue; in the dog it is usually golden-yellow in the middle, brilliant green at the periphery (Nicolas and Gray). Gray, however, points out that the tapetum of the dog varies greatly in colour owing, as he says, to inbreeding.

The function of the tapetum is to enable animals to see better in a dim light; it cannot, of course, enable them to see in the dark. It acts as a concave reflector to the sensitive layer of the retina, so that the rays, having passed through the retina, are reflected back to it by the tapetum. In this way the retina is twice impressed. This is the view expressed by Johnson, who, however, thinks that in animals with a tapetum the usual image is formed, not on the retina, but on the tapetum, and from there reflected forward on to the innermost layer of the retina.

The **Ciliary Body** (Fig. 166) is a large, deeply pigmented, ring-like structure with stellate processes, placed at the anterior part of the globe; the processes indicate the termination of the choroid as a tunic. The ciliary body is attached at its circumference to the sclerotic; it is pierced centrally by a circular opening into which is fitted the lens of the eye. The **ciliary processes,** numbering a hundred or more in the horse, give the part a pleated appearance, and resemble the laminæ of the feet. The processes are not all the same length, those on the nasal side being much shorter than elsewhere. Fig. 166 shows the ciliary zone or body in section; it is wedge-shaped, the base being on the circumference of the ring. Fig. 169 shows it viewed from behind. It was Henderson* who first pointed out the advantage of the ciliary processes being short on the nasal side, thereby enabling an animal to see out of the 'tail' of its eye by permitting the retina to be prolonged forward, by which means the outer boundary of the field of vision is extended.

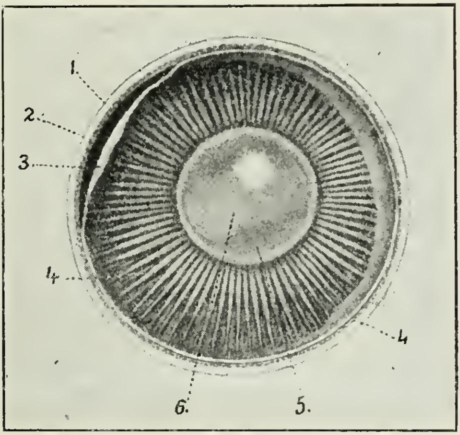

Fig. 169.—Inner Surface of Anterior Part of Left Eyeball of Horse (Equatorial Section) (Sisson-Ellenberger).

1, Sclerotic; 2, choroid; 3, retina (drawn away from choroid); 4, the ciliary processes, which it will be noted are much shorter on the nasal side; 5, crystalline lens through which the pupil (6) may be seen.

The use of the ciliary body, together with its processes, is to furnish an immovable diaphragm to the eye, and so complete the dark or vitreous chamber; it also provides the setting into which is fixed the lens, which is adjusted on the ends of the ciliary processes (Fig. 166); further, it secretes the fluid found in the anterior chamber of the eye, and nourishes the vitreous in the dark chamber. By its pleated or laminated structure it gives attachment to the *zonule of Zinn.* This is a portion of the hyaloid membrane of the vitreous to which the capsule of the lens is attached. The zonule digitates with the processes much as the laminæ of the feet digitate, and the lens is thereby secured in its setting. The ciliary body and processes are highly vascular and deeply pigmented.

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* 'Note on the Comparative Anatomy of the Ciliary Region,' T. Henderson, M.D., *British Medical Journal*, November 4, 1911.

The **Iris** is the movable diaphragm of the eye placed behind the cornea and in front of the ciliary body and processes (Fig. 166). It is part of the ciliary body, but a space, known as the *posterior chamber,* exists between it and the processes; this posterior chamber is a portion of the anterior chamber of the eye, and the aqueous humour has free access to it. The iris in all the domestic herbivora is of a brownish tint—deeply brown in the horse, of a brighter brown in the ox, and brownish-yellow in the sheep. In the dog it is brown or golden-yellow, in the cat greenish or amber, and in the pig a grey-brown or yellow-brown, sometimes bluish. Occasionally the iris of the horse shows partial or complete albinism, as in the so-called 'wall-eye.' In cream-coloured horses it is wholly without pigment, and in piebalds the same will be found, unless there are splashes of black on the face near the eye, in which case it may be partly or wholly pigmented. In the foal the iris is grey, the pigment appearing later.

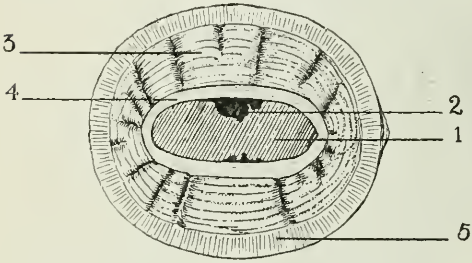

FIG. 170.—BLEACHED IRIS OF THE HORSE.

1, Pupillary opening; 2, corpus nigrum; 3, iris showing wrinkles and pleats in its structure; 4, circular muscle surrounding the pupillary opening; 5, *Ligamentum Pectinatum.*

In the centre of the iris is an opening known as the **Pupil.** This opening is horizontal in the domestic herbivora and pig, vertical and elliptical in the cat, circular in the dog. The pupil is capable of movement; it contracts in bright light and dilates in low degrees of light; this movement is brought about by two unstriped muscles, a circular and a radiating, each of which has a separate nerve-supply. The circular muscle contracts the pupil, the radiating dilates it. The bleached iris of the horse is shown in Fig. 170; the circular muscle is seen surrounding the pupillary opening; the dilator muscle is on the posterior face (Nicolas and Gray), and produces the wrinkles and pleats shown in Fig. 170 on the anterior face; the posterior face of the iris is smooth. In a contracted condition the iris is in contact with the lens. As a consequence, it is not placed vertically in the eye, but bulges forward, so that in hardened specimens it is convex on its anterior and concave on its posterior face (Fig. 166). Though we have stated that stimulation of the retina by light is the natural method by which alterations in the size of the pupil are effected, in the horse this is not strictly true. In direct sunlight the pupil is a mere chink, but in ordinary diffused daylight it barely responds, or should it contract it does so but slightly. Even when diffused light is concentrated on the eye by means of a mirror the iris remains practically unchanged; under the influence of artificial light it actually dilates. This permits the fundus of the eye of the horse being examined ophthalmoscopically without the use of atropine. In all herbivora the pupil is relatively sluggish in response to the stimulus of light, the contraction being greater in the exposed than in the opposite eye. In the cat the reaction of the pupil is brisk and sharper than in the dog. Harris* regards the sluggish pupil of herbivora as indicating a low standard of visual acuity, and considers that this is compensated by greater keenness of hearing and smell. He points out that they are animals which are hunted instead of hunting, and that hearing and smell with them give earlier indications of approaching danger than sight. The shape of the pupil even is in this connection a matter of great physiological interest. An elongated pupil horizontally placed affords a large visual field, such as is required in single-eye vision by animals which are preyed upon; and, as suggested by Matthiessen, it also affords more acute vision for objects peripherically situated in a horizontal field, a great advantage to the herbivora when exposed to attack. The shape of the cornea in these animals is such that the pupil corresponds to its least curved meridian. Very oblique rays of light can enter the eye with a horizontal pupil, especially from the temporal side—*i.e.*, from behind the animal—and, as we have seen previously, the retina is prolonged on the nasal side in order to receive these oblique rays. We have also seen that the pupil must remain horizontal, no matter what position the head assumes, and have studied the method by which this is effected.

In the condition of dilatation the pupil of the horse loses its elliptical shape and becomes circular. It dilates after a gallop; it dilates widely after a violent death, contracting in the course of a few hours until it becomes a mere slit. It also dilates under the influence of atropine and cocaine, and contracts under the effect of morphine and eserine. Dilatation of the pupil is spoken of as *mydriasis*, and contraction as *myosis*. Drugs which dilate the pupil are described as *mydriatics*, and their antagonists as *myotics*. Around the attached margin of the iris—*i.e.*, at the corneo-scleroid junction—a rim of peculiar spongy-looking tissue exists, known as the **Ligamentum Pectinatum** (see Fig. 170).

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* 'Binocular and Stereoscopic Vision in Man and Other Vertebrates,' W. Harris, M.D., *Brain*, part iv., 1904.

It is, of course, a portion of the iris, but quite distinct in appearance; it is traversed by canals, crevices, and spaces, which lead into the lymphatic system of the eye. The function of this tissue is to carry off the aqueous humour which is always being secreted, and so maintain the normal tension of the eyeball.

The **Nerve Supply of the Iris** is through the third cranial nerve, which supplies the circular muscle of the iris, and the sympathetic, which supplies the dilator muscle (Fig. 171). The third nerve, as we have already seen, is intimately connected with the innervation of the voluntary muscles of the eyeball. Through the ciliary ganglion it supplies autonomic fibres to the iris, and its nucleus is linked up with the visual path in the brain. If the ciliary fibres of the third pair be divided, the pupil dilates under the unbalanced action of the sympathetic. The fibres for the radiating muscle, derived from the sympathetic, take a very circuitous course. They arise in the mid-brain and travel down the cord, terminating in cells in the lower cervical region. Here fresh neurones arise, which emerge from the spinal cord by the eighth cervical and first three thoracic nerves, and travel up the neck in the cervical sympathetic, connecting with the superior cervical ganglion; they then pass to the Gasserian ganglion, and by means of the long ciliary nerves in the ophthalmic division of the fifth pair they reach the iris. If the sympathetic supply be divided, the iris contracts under the unbalanced influence of the third pair. In a normal condition both nerves, through the connections of the retina with the brain, are receiving impulses which neutralise each other, so that the iris is responsive to any

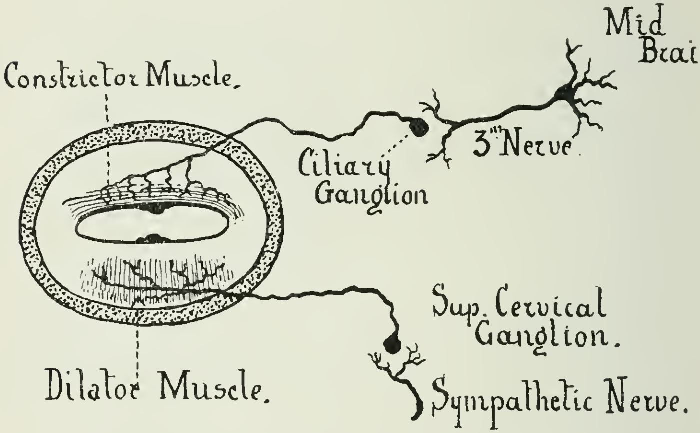

FIG. 171.—NERVE SUPPLY TO IRIS.

excess of impulses which disturbs the balance. The balanced condition is an example of a true reflex act.

In all domesticated animals, but especially well marked in the horse, there exist at the centre of the pupillary edge of the iris one or more black bodies known as **Corpora Nigra** (Figs. 166, 170). They are largest on the upper edge of the pupil in the horse, though a small one may be seen on the lower edge. Johnson, who studied the comparative anatomy of these bodies, pointed out that in the camel there was an upper and a lower row, which interlocked when the pupil was fully contracted. In the horse, when the pupil is strongly contracted in direct sunlight, these particles of 'soot' divide the horizontal pupil into an inner and an outer portion. It would appear that this double pupil might cause an imperfect image to be imprinted on the retina, but on subjecting the question to actual experiment with the camera, no broken image was found. The use of these bodies is to absorb rays of light, but their position on the centre of the pupil would not appear to be the most suitable one for this purpose, and they possibly have some other function.

Lying outside the ligamentum pectinatum and the ciliary body is a narrow rim of tissue known as the **Ciliary Muscle** (Fig. 166); it is of the involuntary type. In all animals it is small as compared with the same muscle in man, and its fibres are mainly longitudinal, whereas in man they are both longitudinal and circular. This muscle is connected with the important question of *accommodation*, or the focussing of the eye for near objects, and will be again referred to when this subject is dealt with. The nerves of the ciliary muscle are derived from the short ciliary branches of the third pair, and issue from the ciliary ganglion. It will be seen that the third pair of nerves is connected with movements of the eyeball, of the iris, and of the ciliary muscle. This is no accidental circumstance, but co-ordinates the direction of the eyes with the closure of the pupil and the contraction of the ciliary muscle; these are simultaneous movements necessary to the act of accommodation. In man the constrictor fibres of the iris and the fibres of the ciliary muscle are paralysed by atropine, but in the horse, dog, cat, and other animals, the ciliary muscle is not paralysed by this alkaloid, though it acts, as it does in man, on the constrictor fibres of the iris.

The **Retina** is an outgrowth from the brain, placed in the orbit for the purpose of receiving the picture of the outside world. It retains its connection with the brain by means of a large stalk, the optic nerve. It is merely a receptive surface, and constitutes, according to the modern classification of nerves, a receptor organ, which, in point of age, is the oldest but one of the primitive brain.

Though it receives the picture it cannot see it; that is effected by a special area of the brain. If this area be damaged, sight is lost, though the retina may be in perfect working order. The *optic nerve* arises from the external geniculate body, the posterior portion of the optic thalamus, and the anterior corpus quadrigeminum; by means of the optic tract the fibres proceed from the brain, converging towards the tract from the opposite side, and meeting it in the *optic chiasma* or *commissure* (Fig. 172). At the commissure the majority of the fibres cross, so that right brain fibres pass to the left eye, and *vice versa ;* about one-sixth of the fibres in the horse do not cross, but proceed direct—*i.e.*, right brain to right eye. This crossing of the nerves is a question of physiological interest and clinical importance. In animals with eyes laterally placed—*i.e.*, fishes, amphibia, reptiles, and birds—there is complete decussation—that is, all the fibres from the right brain pass to the left eye. In all animals higher than these there is partial decussation, as the eyes are not so laterally placed; at first only a small number of fibres pass *direct—i.e.*, right brain to right eye—but as the monkey and man are approached a considerable number of fibres pass direct—about two-fifths in man. Here vision is two-eyed and forward; in a lateral direction it is imperfect. The optic nerves, which gain exit from the cranium *en route*, proceed from the chiasma to their respective eyes, diverging more and more as they approach the eyeballs; before reaching the sclerotic they make a dip of about half an inch (see p. 575), and penetrate the globe *low* down and to the temporal side of the posterior pole of the eye. The nerve is constricted as the result of penetrating the sclerotic (Fig. 166), and having reached the choroid it loses its stalk-like character and expands into a large gauze-like veil,

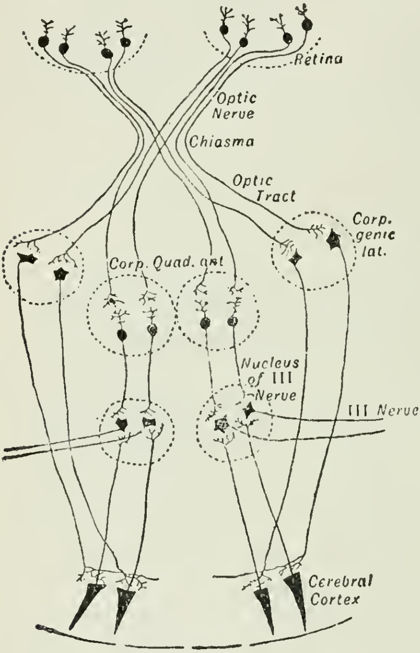

FIG. 172.—SCHEME OF THE VISUAL PATH (HALLIBURTON, AFTER SCHÄFER).

the retina. This change from solid nerve to a flocculent-looking membrane occurs at the **optic papilla,** which is situated on the choroid (see Plate I., Fig. 4, and Fig. 166). The papilla is about 5 mm. in width and 3·5 mm. in depth in the horse, in which animal it is ovoid; in most others it is circular. The optic papilla is found below the tapetum in the pigmented area; it lies so deep in the eye of the horse that it can be seen with the ophthalmoscope only by looking downwards over the lower margin of the pupil.

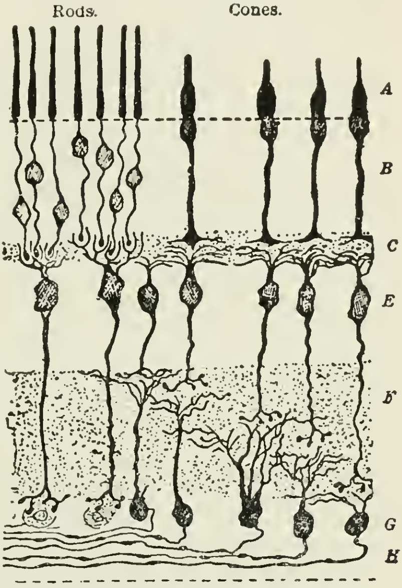

Fig. 173.—Diagram of Structure of Retina (Bowditch, after Cajal).

A, Layer of rods and cones; *B*, external nuclear layer; *C*, external molecular layer; *E*, internal nuclear layer; *F*, internal molecular layer; *G*, layer of ganglion cells; *H*, layer of nerve fibres.

The retina consists of many coats, the only one connected with vision being that which, excluding the pigmentary layer, is farthest from the light, and consequently nearest to the choroid. This layer is known as that of the *rods and cones* (see Fig. 173); these are the essential visual elements of the retina; whenever they are absent the part is insensitive to light, as, for example, at the optic papilla, which is blind. Each cone is connected with a single nerve-cell, but there may be only one nerve-cell to several rods; the cone is consequently regarded as offering a more direct conducting path than the rod. Over the area of most acute vision in man cones only are found—for instance, at the *fovea centralis*, which is absent in all animals below man and the higher apes, with the exception of certain birds. Here the retina is thinned out until nothing but cones remain. This is in the centre of the field of vision in man; it is a little to the temporal side of the optic disc, and visual acuity diminishes rapidly as the image falls away from the fovea or region of *central vision*. The field of vision outside the central is known as the *peripheral* or *excentric* field; another term for it is the *panoramic* field. In the lower animals there is no means of knowing with precision which area of the retina is the most sensitive, but it is possible to arrive at a conclusion indirectly. Most of the herbivora raise and draw back the head when staring intently at an object; this is especially well seen in the horse, who appears to draw his body up as if collecting himself for a sudden move, at the same time raising the head high. In this attitude the area of the tapetum may be regarded as that of acute vision, and we may consequently look upon the optical axis of the eye as agreeing with the visual axis.

It is in the rods and cones that the primary conversion of light vibrations into visual impulses takes place. The rods contain a pigment known as **Visual Purple** or *Rhodopsin*, which is readily decomposed by light, especially by the blue and violet rays, by which the pigment is decolourised. The colour is regained in a dim light. The perception of colours, a question which will be dealt with later in considering the theory of vision, is not due to the rods. The cones are regarded as the visual cells in bright light, and provide acute vision; the rods are adapted for dim light, as is proved by their decolourisation by a bright light, and the fact that they are numerous in animals which seek their food by night. It is the tapetum and the rods which enable feline animals to prey by night, and the same structures enable the herbivora to find their way and move freely in what to us is darkness.

As the rods and cones are nearest to the choroid, while the nerve fibres and cells are nearest to the vitreous, it follows that light has first to traverse the retina to reach the visual layer, and is then reflected by the tapetum; the impulses set up in the rods and cones then travel towards the vitreous in order to reach the nerves which subsequently form the optic. The whole area of the retina is sensitive up to the ciliary processes; in fact, it has been shown that in the horse and other animals the rods and cones are better developed in the temporal peripheral zone than elsewhere, probably, as Nicolas and Gray remark, in connection with binocular vision. There is no tapetum, or rather none exposed in the peripheral zone, it being covered by the dense pigment of the retina; it is obvious that reflection cannot occur here. We may therefore assume that night vision in animals is central, and not peripheral.

The **Lens** fits into a circular setting formed by the ciliary processes, and there rests upon the broad edges of the processes (Fig. 166). It is contained in a capsule; the capsule is attached to a *suspensory ligament*, formed by the hyaloid membrane of the vitreous known as the *zonule of Zinn*; this ligament firmly digitates with the ciliary processes, and in hardened specimens, if the lens be removed from its setting, points will be seen around its equator where the zonule is attached. The lens is biconvex, the convexity of the posterior face being greater than that of the anterior in herbivora, while the converse is true of felines. In the horse its antero-posterior diameter varies; we have found it 10·5 mm. to 14 mm. ($\frac{3}{5}$ to $\frac{3}{4}$ inch). It is made up of many onion-like layers, each having a different refractive index and different curvature. Its mean refractive index in the horse and dog is 1·49; in man it is 1·39. Its focal length in the horse is 15·5 diopters ($2\frac{1}{2}$ inches), while that of the cornea is 12·6 diopters ($3\frac{2}{10}$ inches) (Nicolas and Gray), so that the lens of this animal (and the same remark applies to the dog) refracts more than the cornea, which is the reverse of what occurs in man. The lens is an elastic body, as may be seen by puncturing its capsule when the lens becomes herniated; by means of its capsule it is kept in a state of tension. The capsule being attached to the suspensory ligament, and the latter dovetailing with the ciliary processes, the lens is flattened when the capsule is pulled upon, and bulges of its own elasticity when the tension is removed. A further study of the question of the alterations in the shape of the lens will be made when dealing with accommodation.

The **Humours of the Eye** are the *aqueous* in the anterior chamber, and the vitreous in the dark chamber. The *aqueous humour* is generally regarded as a secretion by the ciliary processes, some say from the iris; others regard it as a filtrate from the blood. It bathes the tissues in the anterior chamber, and in it are immersed the whole of the iris, the anterior surface of the ciliary processes, the anterior face of the lens, and the posterior face of the cornea. Chemically it is a watery fluid poor in solids, and is in reality lymph. It is carried off as rapidly as formed through the lymphatic channels of the ligamentum pectinatum, which communicate with the veins. The fluid in the anterior chamber is always under pressure equal to 25 mm. of mercury; this maintains the curvature of the cornea. The same pressure which keeps the cornea curved is exerted on the anterior face of the lens and on the two surfaces of the iris. Owing to this pressure, if the cornea be punctured, the fluid spirts out some distance. The cornea now collapses, and a portion of the iris even may protrude, but so rapidly is the fluid secreted that in about twenty-four hours the curvature of the cornea is restored, and in a day or two the puncture is invisible (unless the iris has been detained in the wound). After death the process of drainage appears to continue, while that of secretion ends, so that the cornea shrinks and the anterior chamber collapses. The lymphatic drainage of the anterior chamber sometimes fails through blocking of the channels. This gives rise in man to excessive tension of the eye (*glaucoma*), which becomes of stony hardness, and total loss of sight follows unless the tension is relieved. The aqueous humour is prevented from exercising any injurious effect on the cornea by the epithelium and lining membrane of the chamber, the *membrane of Descemet*, which is more glass-like than the cornea itself. The refractive index of the aqueous humour is the same as that of the cornea (1·377).

The **Vitreous Humour** is totally different in appearance from the aqueous, being like molten glass. It is enveloped and intersected in all directions by a membrane, the *hyaloid*, which prevents it from coming into actual contact with the retina. Anteriorly this membrane is arranged to form the suspensory ligament of the lens, as already described. The vitreous contains much mucin and a small percentage of solids; its refractive index (1·335) is much the same as that of the aqueous. Its chief function is to maintain the intra-ocular pressure in the dark chamber and keep the delicate concave retina in position. By its pressure on the lens it keeps the suspensory ligament in a condition of tension, its usual state, as it is only for near objects that any relaxation of this tension is required.

The **Visual Areas** in the brain must now be considered. In animals possessing the old primitive brain—fishes, for example—the visual path terminates at the mid-brain, as these animals possess no cerebrum. As the scale of animal life is ascended and the cerebrum develops the visual path extends from the mid-brain to the cerebrum, where a visual region arises in the occipital portion. The neurone system is as well marked in the eye as elsewhere (see Fig. 172); the first neurone exists between the retina and mid-brain, the optic fibres being axons of the nerve-cells of the retina. By synapses these are connected with a second neurone, from which issues the *occipito-thalamic fibres*, running from the mid-brain to the cerebrum (see Fig. 153, p. 523). The visual cortex is situated in the occipital region of the cerebrum, in the area known as the calcarine fissure. Here is found a white line, known as the *line of Gennari*, which represents a layer of special nerve-fibres placed in the grey substance of the cortex. This line, which can be readily traced, encloses an area known as the **visuo-sensory**. The size and complexity of structure of the area increases as the animal scale is ascended. Mott* points out that the more the animal depends on vision as a directive faculty in its preservation, the more complex the structure of the visual cortex becomes. Thus the pyramidal layer of cells in the visual area forms a deep layer in the cat, less deep in the dog, and this he regards as associated with an increase in the perfection of binocular vision. On to the visuo-sensory areas the retinæ are projected, not, it will be observed, by retinal fibres, but by those from the mid-brain (Fig. 172), the right occipital lobe receiving the picture from the two right halves of the retina, the left lobe receiving that from the two left halves (Fig. 174). If a visual area be removed experimentally, blindness results in the two halves of the eye which are represented. The visuo-sensory area receives the picture, but it does not *interpret* or *elaborate* it. This is effected in an area immediately outside the visuo-sensory, known as the **visuo-psychic,** a part possessing special peculiarities in structure as compared with the sensory area, though in animals this is not nearly so well marked as in man.

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* 'The Progressive Evolution of the Structure and Functions of the Visual Cortex in Mammalia,' by F. W. Mott, M.D., F.R.S., *Archives of Neurology*, vol. iii., 1907.

We have seen that in animals with binocular vision the right visuo-sensory area receives the visual impressions from the right half of the retina of each eye, the left lobe receiving the impressions from the two left halves. In pure monocular vision the left brain receives the visual impressions from the right eye, the right brain those from the left eye, so that two distinct pictures are formed at one and the same time. This crossing of the visual picture is effected at the optic chiasma. With animals—for example, the horse—where the vision is commonly monocular, but also frequently binocular, it is doubtful how the visual impressions in binocular vision are received. In these cases, as will be shown presently, the two right halves and two left halves of the retina cannot correspond owing to the width between the eyes.

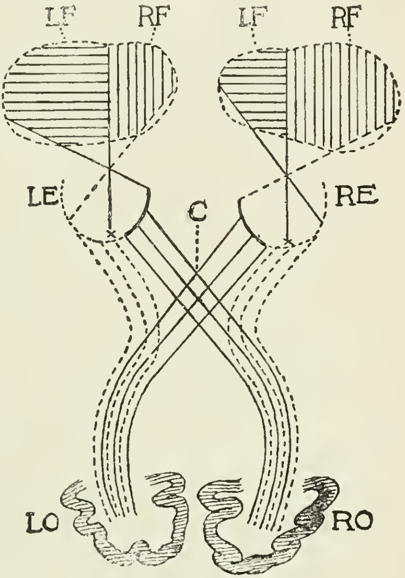

Fig. 174.—Diagram of Relations of Occipital Cortex to the Retina in Man (Stewart).

RO, LO, Right and left occipital lobes; RE, LE, right and left retina; C, optic chiasma; RF, LF, right and left visual field of each eye. The continuous lines passing back from the retinæ to the occipital cortex represent the crossed, the broken lines the uncrossed, fibres of the optic nerves and tracts. The intermediate stations on the visual path shown in Fig. 172 are omitted.

Accommodation.—All rays of light proceeding from a distant object may be regarded as parallel, and all those proceeding from an object within 6 metres (20 feet) of the eye may be regarded as divergent. A distant object is one situated anywhere between 20 feet from the eye and infinity; an object closer than 20 feet to the eye is called near, and this point extends in man up to 10 to 13 centimetres (4 or 5 inches), at which distance no object can any longer be distinctly seen. The nearest distance at which objects can be distinctly seen is called the *near point*. Parallel rays need no focussing on the retina, but rays from near objects require focussing owing to their divergent nature; it is evident that the nearer the object to the eye the greater the focussing required. This focussing is brought about by a change in the shape of the anterior surface of the lens; it becomes more convex for near objects, and this increase in convexity is due to the ciliary muscle drawing forward the choroid coat, and with it the ciliary processes. By this means the tension normally exercised through the zonule of Zinn (the suspensory ligament of the lens) is relaxed, and the lens of its own inherent elasticity bulges forward, and so increases the curvature of its anterior face (Fig. 175). A more convex lens is a more convergent one, and its focus is therefore shorter; in this way the images of near objects are brought to a focus on the retina and distinctly seen, whereas if this increase in curvature had not taken place, the image would have been focussed behind the retina. The power the eye possesses of focussing itself is known as the mechanism of accommodation; the explanation given above is that of Helmholtz for the human eye, and is the one generally accepted.

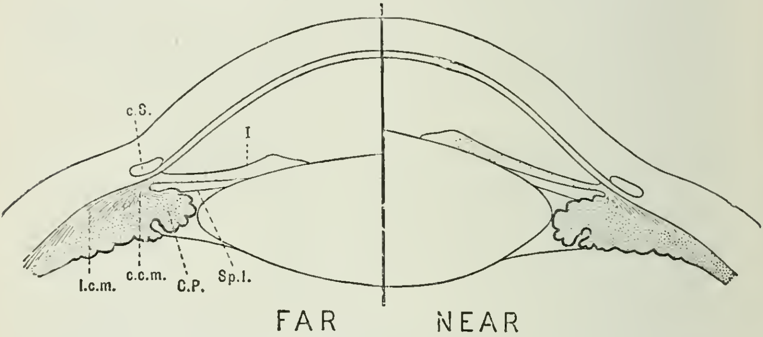

Fig. 175.—Diagram to illustrate Accommodation (Foster, after Helmholtz).

C.P., Ciliary process; I, iris; Sp.l., suspensory ligament; l.c.m., longitudinal ciliary muscle; c.c.m., circular ciliary muscle; c.S., canal of Schlemm. The left half represents the shape of the lens for viewing distant objects, and the right half that for viewing near objects.

It is by no means certain that the mechanism of accommodation in animals is the same. Their ciliary muscle is insignificant, though this may be due to the fact that the work it is called upon to perform is not of an exacting type. The objects which a horse looks at within 20 feet of the eye are ordinarily not such as to require any great effort in accommodation. In jumping he must accommodate, and his vision must be precise; in the stable objects are very near, and we know that he avoids them, showing that accommodation occurs, but all of these are large objects compared with reading type. He requires no acute vision for food, for he feeds by the sense of smell. It may, therefore, be that the thin rim of ciliary muscle suffices, assuming the Helmholtz theory applies; but we are personally more inclined to think that the lens undergoes no important alteration in curvature, but rather that the distance from the posterior face of the lens to the retina is capable of alteration, and this would be just as effective for the purpose of focussing as an alteration in the thickness of the lens. Such a mechanism may be supposed to exist in the muscles of the eyeball. This takes us back to the theory of accommodation held before the days of T. Young, when it was thought that the straight muscles squeezed the eye about its equator, thereby increasing its antero-posterior diameter, and so carrying the retina backwards. Young announced 120 years ago that the lens was the focussing medium of the eye, and not the ocular muscles. Nevertheless, in animals, especially the horse, the retractor muscle is of extraordinary size, and out of all proportion to the function of occasionally withdrawing the eyeball within its socket. It completely surrounds the globe, and runs a long way forward on its surface; it seems probable that by means of the ocular muscles accommodation is effected. The shape of the eyeball of the horse, as seen in Fig. 166, suggests that under muscular compression it would lend itself to elongation, especially as *an alteration of a few millimetres only is required.* In fishes it is known that there is a muscular arrangement which pulls the lens towards the retina, and in amphibia and snakes accommodation is brought about by changes in intra-ocular pressure. One other argument against the ciliary muscle theory of the focussing of the eye is that in the lower animals the muscle is not paralysed by atropine. In man the iris dilates and the ciliary muscle is paralysed, so that accommodation for near objects is impossible. In the horse and other animals the iris dilates, but it is impossible to paralyse the accommodation as judged by the fact that the animal is capable of seeing near objects and of avoiding obstructions. This is strong evidence in favour of some method of accommodation existing in animals below man and the monkey other than the one generally accepted.

Catoptric Test.—As bearing on the question of accommodation, reference must be made to the reflections which are seen in the eye when a lighted candle, for example, is held up before it. Three reflections of the candle are seen; a very sharp, large, and bright one from the cornea; a second, duller and smaller, which is reflected from the anterior face of the lens; and a third, very small, brighter than the middle image, and *inverted*, which is reflected from the posterior face of the lens (Fig. 176); these are known as the Purkinje-Sanson images.

In a normal eye all three images are distinctly seen, and equally visible at any point on the reflecting surfaces. When the candle is moved from side to side, and up and down, the images follow it, the two upright moving in the same direction as the candle, the inverted image moving in the opposite direction to the candle. This phenomenon has been taken advantage of in determining the freedom of the lens from opacity (cataract); though superseded by the greater accuracy of the ophthalmoscope, it is still a valuable aid. In cataract one or more of the reflections become blurred, and sometimes the blurred image is duplicated.

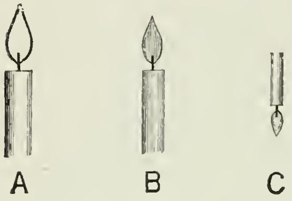

FIG. 176.—DIAGRAM OF THE CATOPTRIC TEST.

A, From the anterior surface of the cornea; B, from the anterior face of the lens; and C, from the posterior face of the lens. In the diagram, B and C should have been shown as nearer together.

The first and second images are erect, inasmuch as they are reflected from a convex surface; the third image is inverted, as it is reflected from the posterior surface of the lens, which, when viewed from the front, is concave. If, therefore, the lens of the horse alters in curvature, as does that of man, in accommodating for a near point, the middle image, when accommodating, will come nearer to the corneal image, and become smaller as the lens becomes more convex. It is certain that this does not take place in the horse.

Physiological Optics—*Passage of Light through Lenses.*—All rays of light are diverging, but so slight is the divergence of the rays from distant objects that for the purposes of the eye they are regarded as parallel. All rays proceeding from an object situated at from 6 metres (20 feet) to infinity from the front of the eye are considered as *parallel rays;* all rays within 20 feet from the cornea are *diverging rays*. Obviously the nearer the object to the cornea the greater the divergence, so that there is more divergence in the rays proceeding from a body 1 foot from the eye than in one 10 feet from the eye; conversely, the farther the object is from the eye the less divergent the rays until that point is reached beyond 20 feet at which the rays may be regarded as parallel.

A convex lens has two curved surfaces, and a line drawn through the centre of these two surfaces is known as the *principal axis* of the lens (Fig. 177, *mm*). The essential idea of a double convex lens is that it is thicker at the centre than at the edges. Situated on the principal axis of a biconvex lens at a point in its interior is the *optical centre* (Fig. 177, O); any other straight line passing through the optical centre is termed a *secondary axis* (Fig. 177, *nn*).

When *parallel* rays of light (Fig. 178) pass through a convex lens, they are refracted and brought to a point *f* on the opposite side of the lens, known as the principal focus; the only rays not refracted are those passing through the centre of the lens—viz., those coinciding with the principal or secondary axes. The converse of this is also true—viz., *divergent* rays proceeding from the principal focus of a lens *f* pass through and are rendered parallel (Fig. 178).

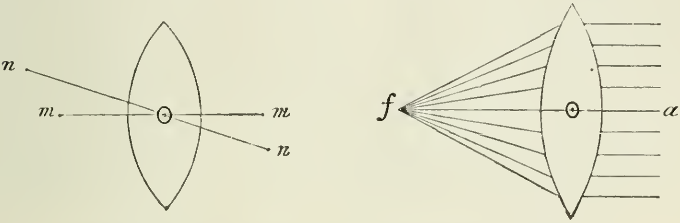

FIG. 177. FIG. 178.

FIGURES ILLUSTRATING THE ACTION OF LENSES UPON RAYS OF LIGHT PASSING THROUGH THEM.

Fig. 177.—Biconvex lens: O, optical centre; *mm*, chief or principal axis; *nn*, secondary axis.

Fig. 178.—Parallel rays, *a*, are refracted and brought to a focus at *f*. Divergent rays from *f*, on passing through a convex lens, are rendered parallel.

The distance from O, the optical centre of the lens, to *f*, its principal focus, is known as the focal length of the lens. If the divergent rays, instead of proceeding from the focus of the lens, proceed from a point *l beyond the focus* (Fig. 179), then the rays, on passing through the lens, are not rendered parallel, but *convergent* (as the refractive power is more than sufficient to render them parallel), and they come to a focus again on the other side of the lens at the point *v*. The distance from the lens at which they come to a focus depends upon the distance of the luminous point *l* from the lens on the opposite side; thus the nearer the luminous point *l* to the principal focus *f*, the farther will the focus on the opposite side recede, and *vice versa*. The two foci *l* and *v* are termed *conjugate foci*, and they

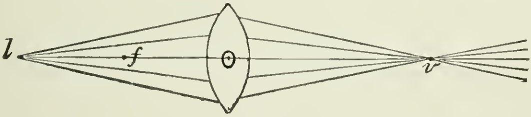

FIG. 179.

Rays of light passing through a convex lens from *l* at a point beyond the focus *f*, cross at some point *v*, and invert the image.

bear a definite relationship to each other. If the rays of light proceed from a point L (Fig. 180), which is nearer to the lens than the principal focus F, the lens is unable to refract the rays sufficiently, and they issue from the opposite side divergent, as *dd*.

Parallel rays of light passing through a *concave* lens, instead of being refracted to a focus, are bent and become divergent, so that a concave lens has no real focus; but if the divergent rays be produced backwards so as to meet on the principal axis of the lens, the point where they meet is called the *negative focus* of the lens.

Spherical Aberration.—The rays of light passing through a convex lens are not all equally refracted, those passing through the circumference being more bent than those passing near the centre; the result is that the rays do not all meet in the same point, those passing through the circumference of the lens coming to a focus earlier than those passing near the centre. This defect, known as 'spherical aberration,' is remedied in the eye by the introduction of a diaphragm or iris, which prevents some of the rays of light from passing through the circumference of the lens; spherical aberration is further prevented by the fact that the refractive index of the central part of the lens is greater than that of the circumference. Spherical aberration produces indistinctness of vision by the production of circles of diffusion, caused by those rays which meet too early crossing each other and forming a circle.

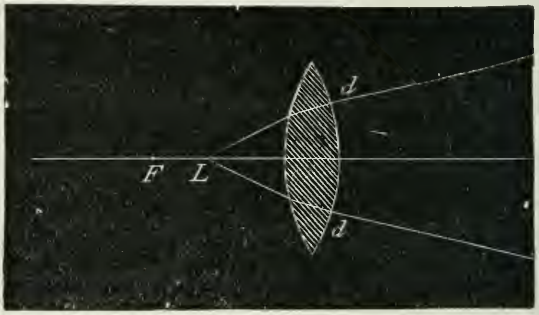

Fig. 180.

Rays of light from a point L, between the focus F and the lens, diverge when passing through a convex lens.

Chromatic Aberration is due to the decomposition of white light into its primary colours by its passing through a prism or a convex lens—*i.e.*, to the formation of a spectrum. The colours of the spectrum are differently refracted, the red being the least bent, the violet the most; when, therefore, the red is distinctly seen, the eye is not focussed for the violet. There is no compensation in the eye for chromatic aberration. The defect is usually not noticeable, because it is small in amount, and is rapidly corrected by alterations in accommodation.

Schematic and Reduced Eye.—When a ray of light enters the eye, it has to pass through four surfaces, and, including the air, four media. There are two surfaces to the cornea, anterior and posterior, and two surfaces to the lens, anterior and posterior; each of these surfaces differs from the others in curvature. As media, there are the aqueous and vitreous humours and the crystalline lens; a further complication is that the last is not of the same refractive index throughout. The formation of an image in such a complex optical system would be difficult to understand, were it not possible to construct theoretically a simplified eye, or, as it is known, *a schematic* eye. The basis of its construction is that, so long as a complex system has its surfaces and media ' centred '—that is, symmetrically disposed around the optical axis—it is possible to consider it as consisting of two surfaces and two media—viz., the *schematic* eye—and even to simplify it still further to one surface and two media—the *reduced* eye—the media being air and water. In such a simple optical system it is readily possible to trace the paths taken by the rays of light, and so understand the formation of an image on the retina of the eye. The reduced eye of the horse, ox, and dog will be found described in works on veterinary ophthalmology.*

Cardinal Points.—The most simple optical system which can be devised has as *optic axis* (OA, Fig. 181)—viz., a line passing through

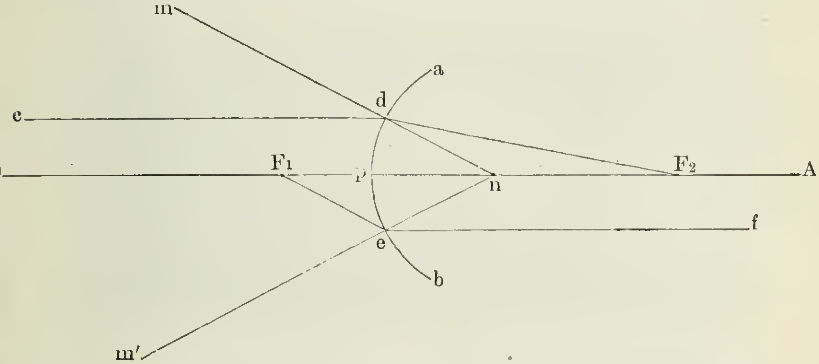

FIG. 181.—THE CARDINAL POINTS OF A SIMPLE OPTICAL SYSTEM (FOSTER).

OA, Optic axis; *apb*, a curved spherical surface; *n*, nodal point; F_2, principal posterior focus; F_1, principal anterior focus; *ef*, rays proceeding from F_1, rendered parallel to the optic axis; *p*, the principal point; the rays *md*, O*p*, and *m'e*, pass through the nodal point *n* and undergo no refraction; the rays *cd*, parallel to the optic axis, are refracted, and meet at F_2.

its centre perpendicular to its refractive surface (*apb*). On the optic axis is situated the centre of curvature of the refracting surface; this centre is known as the *nodal point n*. All rays of light which strike the refractive surface perpendicularly, such as O, *m*, pass through the nodal point and are not refracted; all rays of light *parallel* to the optic axis, such as *cd*, strike the refractive surface obliquely and are refracted, and the point where they meet is called the *principal posterior focus*, F_2. On the optic axis, in front of the refractive surface, is situated a point F_1 known as the *principal anterior focus ;* rays proceeding from this point strike the surface obliquely, and are so refracted as to be rendered parallel (*ef*) to the optic axis (OA). To these must be added the *principal point p*—that is, the point where the refracting surface cuts the optic axis. These various points are known as the *cardinal points* of the simple optical system we have imagined. For a more complex system, such as the eye, even when simplified, there are two nodal points, two principal foci, and two principal points; but with the reduced eye, where there is but one surface and two media, the two nodal points become one, and the two principal points one. In order to be able to calculate the position of the cardinal points of the eye certain data must be known, such as the refractive index of the media, the radius of curvature of each refracting surface, the distance from the cornea to the lens, and the thickness of the latter.*

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* See Nicolas and Gray.

Formation of a Retinal Image.—We are now in a position to understand the formation of an image on the retina. Rays of light entering the eye, as from the arrow XOY (Fig. 182), issue as a pencil of rays from every point of the arrow; the pencil containing the central ray is known as the principal ray. All principal rays, *aa′*, pass through the nodal point *n* without undergoing refraction, while the rays *bc* and *b′c′* are refracted to a greater or less extent, so that in this way the retinal image becomes inverted, and very much smaller than the object it represents; it is a miniature though perfect representation of the object presented to the eye. The chief refraction in man occurs at the cornea, but in the horse and dog, and probably all domesticated animals, the lens refracts more than the cornea (Matthiessen). A man may have good distant vision without a lens, for, as we have seen, its chief function is connected with accommodation, but in the lower animals this is not the case, so far as can be judged by the removal of the lens in cataract. The other media also refract—for instance, the vitreous, but as its index is the same as that of the aqueous, the assistance rendered is not believed to be great.

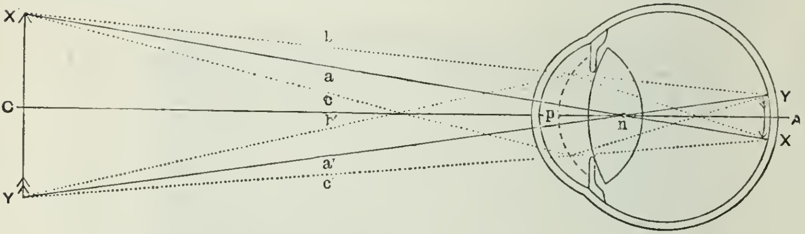

Fig. 182.—Diagram of the Formation of a Retinal Image (Foster).

a, Principal ray of the pencil of light proceeding from X; *a′*, principal ray of the pencil of light proceeding from Y; the principal rays pass through the nodal point *n* without being refracted; the other rays, *bc* and *b′c′*, are refracted and cross behind the nodal point at the principal posterior point. In this way the arrow XY forms a smaller inverted image of an arrow on the retina YX. OA, optic axis.

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* See Nicolas and Gray for an account of the cardinal points of the eyes of animals.

Though the retinal picture is so completely inverted that the right hand of the object becomes the left of the image, and the top becomes the bottom, yet the mind does not perceive the image as inverted, but mentally refers the picture, not to the retina, but back to the object. In Fig. 182, the angle X*n*Y is equal to the angle Y*n*X. The angle X*n*Y is spoken of as the *Visual Angle*, and all objects having the same visual angle form the same sized picture on the retina. By the aid of the visual angle the size of an image on the retina may be calculated, provided the distance of the nodal point from the retina is known. Thus at the distance of a mile, a man 6 feet high is represented on the retina of a horse by an image $\frac{1}{880}$ of an inch in height; in the human eye at the same distance the picture of the man would be $\frac{1}{1500}$ of an inch, or about the size of a red blood-corpuscle.

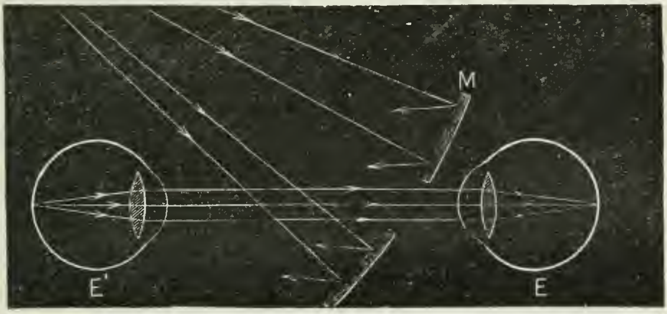

FIG. 183.—DIRECT METHOD OF USING THE OPHTHALMOSCOPE (STEWART).

Light falling on the perforated concave mirror M passes into the observed eye E′; and, both E′ and the observing eye E being supposed emmetropic and unaccommodated, an erect virtual image of the illuminated retina of E′ is seen by E.

The nearer the object the larger the image; taking the 6-foot man again at a distance of 10 yards, his height on the retina of the horse would be $\frac{1}{5}$ of an inch, whilst on the retina of a man it would be rather over $\frac{1}{8}$ of an inch. From this it is obvious that the horse with normal sight sees the same image more clearly than a man, for the reason that it produces a larger picture on his retina.

The Ophthalmoscope.—This instrument is employed in examining the interior of the eye. It consists of a mirror with a hole in its centre, which is applied to the eye of the observer, so that he can see through the hole, and rays from a suitable source of light are reflected from the mirror through the pupil of the eye under examination. These rays are reflected back through the pupil of the observed eye, and entering the hole in the mirror, pass into the eye of the observer (see Fig. 183).

A brief account of the fundus of the eye when examined by the ophthalmoscope has been given at p. 576. It is a magnified image, the refractive media of the eye making it appear about eight times larger than it actually is.

Errors of Refraction.—An eye which possesses the power of seeing an object distinctly from the near point—*i.e.*, a few inches from the eye—to infinity is known as *emmetropic*; it is the perfect eye (Fig. 184, 1). All eyes do not possess this range of vision owing to the length of the eyeball. Where the distance from the lens to the retina is too considerable, the eye is *myopic*; the image comes to a focus in front of the retina, and only a confused and blurred image is formed on the screen (Fig. 184, 3). Where the distance from the lens to the retina is too short, the retina is in front of the focus formed by the refractive media, and the picture is not distinctly seen as the focus falls behind the retina (Fig. 184, 2); such an eye is termed *hypermetropic*. These defects are remedied in the human subject by employing a concave glass (which scatters rays) for the myopic eye, and so preventing the focus from forming too early; while a convex

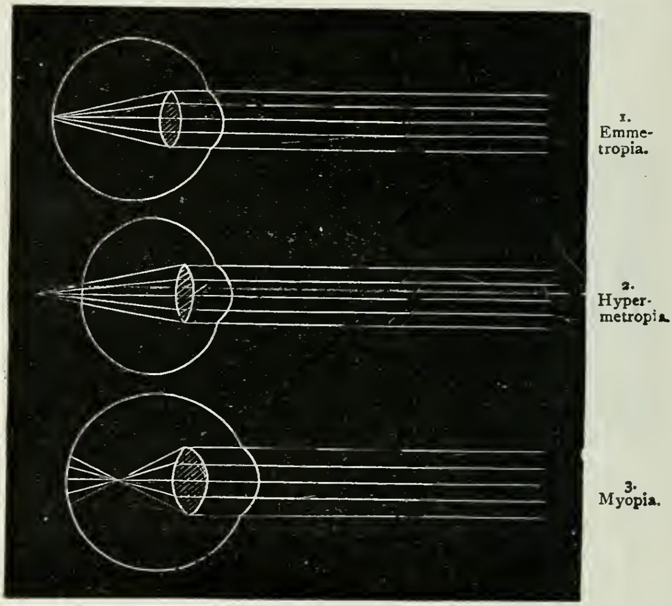

FIG. 184.—DIAGRAM OF AN EMMETROPIC, HYPERMETROPIC, AND MYOPIC EYE, TO ILLUSTRATE WHERE THE FOCAL POINT EXISTS (HALLIBURTON).

In 2 the short eyeball causes the focus to form behind the retina; in 3 the long eyeball causes the rays to come to a focus in front of the retina.

lens is employed for the hypermetropic, as it brings the rays of light to a focus earlier than would otherwise happen.

There is another defect due to irregularities in the curvatures of the cornea, the curvature of the horizontal meridian not agreeing with that of the vertical. The cornea, in other words, is flatter in one of its meridians than in the other (p. 574), so that the rays of light which pass through one meridian of the eye are brought to a focus before those traversing the other meridian. This condition is known as *astigmatism*.

Myopia, hypermetropia, and astigmatism may occur in the eyes of the domesticated animals. The horse, according to the writer's observations,* is commonly myopic and astigmatic, though the degree of error is small. Early work in Germany described him as hypermetropic, but all later researches point to myopia as being very much more frequent than hypermetropia. G. L. Johnson† regards the myopia of the horse and rabbit as due to domestication, and says the condition is almost unknown in wild animals. The dog is also regarded as myopic, probably for the same reason. The dog certainly does not give one the impression of being myopic, so that it is probable the error is small. Lang and Barrett, in their examination of the refractions of wild animals, found hypermetropia to be frequent, and Johnson found the same condition throughout the wild mammalia. The amount of hypermetropia commonly found by him was under 1 diopter (40 inches), which is practically negligible. Emmetropia he met with very rarely, and this agrees with the writer's observations on the horse; similarly, in the horse Johnson found astigmatism to be a common error; indeed, he says this error occurs universally in the domestic animals, and throughout the *ungulata*, cetacea, and all mammals below them.

Monocular and Binocular Vision.—Whether an animal can see an object with both eyes or only with one is, broadly speaking, determined by the position of the eyes in the head. Binocular vision requires that a pair of eyes shall be so placed as to be capable of converging on an object and seeing it as a single, and not as a double one. Eyes situated close together are obviously necessary for this purpose, and true binocular vision is defined as single vision with a pair of eyes, the two eyes acting as one. Eyes situated close together afford acute vision, and are the complement of skilled fore-limb movements; the hand in man, the paw in the feline, are accurately directed by means of binocular vision. Eyes laterally placed in the head—*e.g.*, as in the hare and duck—are evidently intended for one-eyed vision.

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* 'The Refractive Character of the Eyes of Horses,' *Proceedings of the Royal Society*, No. 334, 1894.

† *Op. cit.*

Each eye can see a distinct picture at opposite poles of the head, and such vision is known as monocular. But though the eyes of an animal may be situated at the sides of the head, it does not follow that it cannot see to the front. The prominence of the eye and shape of the head here play an important part; when a duck swims or waddles towards one, he keeps the head true to the front and sees out of both eyes; the hare can do the same, and certainly can see her pursuer out of 'the tail' of both eyes. Whether the vision with both eyes is identical in character with binocular vision in man cannot at this point be discussed. An animal with the eyes laterally placed may have these located so far forward that, though vision is usually monocular, it may also be two-eyed. The horse will occur to the reader as belonging to this group, but in this animal there is limited backward vision with both eyes (see p. 574), though by slightly turning the head he can obtain a larger field behind, but only with one eye (Fig. 185). The ox and sheep are unable to see out of the 'tail' of both eyes simultaneously when the head is erect, as the ears come in the way, but when the head is depressed, as in grazing, they can see behind with both eyes, though, as in the horse, the field is limited, for the head is always turned when they wish to obtain a better view.

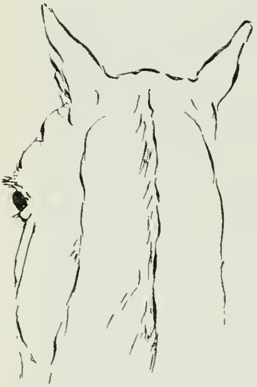

FIG. 185.—DIAGRAM ILLUSTRATING THE EXTENT TO WHICH A HORSE CAN SEE BEHIND HIM.

With the head straight to the front he can see indistinctly out of the 'tail' of both eyes. By the least inclination of the head, as in Fig. 185, a large visual field behind him may be covered.

The conditions essential to binocular vision must now be explained. Each eye projects into space the image formed on its retina (p. 595). When the projected images are superposed and precisely coincide only one object is seen, and not two. This precise superposition of the images in space occurs when the two images formed on the retina fall on what is known as **corresponding points of the retina.** To understand what is meant by corresponding points we must turn to the human eye, and in imagination take out the retina of one eye and lay it over its fellow, but not face to face; the left portion of one will now lie exactly over the left portion of the other, the upper and lower parts equally corresponding. A vertical line, *vm* (see Fig. 186), will now divide them into halves, from which it will be seen that the temporal side, say of the right retina, *b'd'*, corresponds to the nasal side of the left retina, *bd*. In Fig. 186 the two circles representing the right and left retinæ have been further divided into quadrants, *a′b′* in the right eye corresponding to *ab* in the left eye, and similarly for the lower quadrants. It will be observed that the optic nerve, *o*, is in the left segment of the right eye and in the right segment of the left eye. The area of central vision—*i.e.*, the fovea, *f*—will in each retina be in the same place. Every rod and cone in the right eye now corresponds with every rod and cone in the left eye. If we look at an object a little to the right, as at *z*, Fig. 186, it will be seen single, for the reason that the image falls on corresponding parts of the retinæ—*i.e.*, as *z′* on the left or nasal side of the visual axis, *v.l*, of the right eye, and as *z* on the temporal side of the left eye; similarly with *y*; *x* being in the central line of vision, falls on the fovea in each eye at *xx′*.

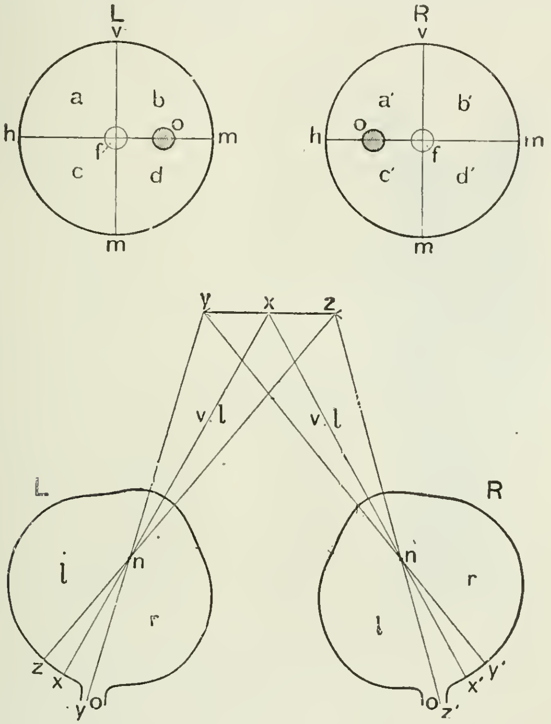

Fig. 186.—Diagram illustrating Corresponding Points in the Human Eye (Foster).

z′ x′ y′ are points in the right eye corresponding to *z x y* in the left eye; *v.l*, visual axis. The two figures illustrate the corresponding points of the retina described in the text.

Bearing in mind what has already been said about the decussating and direct fibres in the optic nerve (p. 582), the probable explanation of corresponding points in the retina of man is to be found in this arrangement; the nerve-fibres from the right half of each retina—*i.e.*, the corresponding halves—meet in the optic chiasma and proceed to the right brain, while the fibres in the left halves proceed to the left brain (see p. 587 and Fig. 174).

Applying what has been said of the corresponding points of the retina to the case of the hare or the bird, which, besides having lateral vision, can also look forward and backwards with a pair of eyes, it is evident to us that binocular vision as above defined does not exist, for the reason that it is impossible for the image to fall on the right halves and left halves of each retina, and be carried to the right and left brain. It falls in these, and in all animals with the eyes wide apart, on the *temporal side of each retina*—*i.e.*, on *opposite* instead of on corresponding sides; not only so, but in the case of the bird there are no direct fibres, so that the picture in the right eye can only be seen by the left brain, and *vice versa*. Is the image in these animals double, or does some different arrangement exist to receive a single image with a pair of eyes where the corresponding points of the retina do not agree? This question cannot be answered. In the case of the dog and the cat there exists binocular vision, as in man.

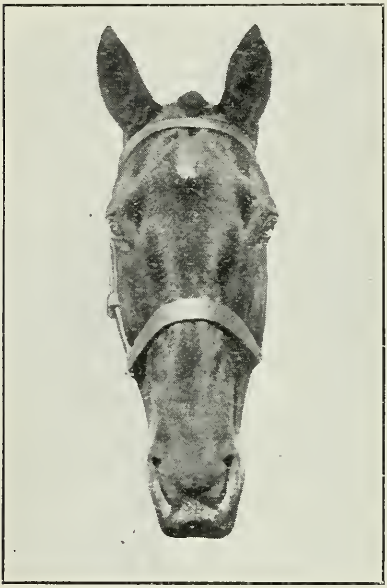

FIG. 187.—THE POSITION OF THE EYES AND ATTITUDE IN BINOCULAR VISION.

Between the group of animals with the eyes laterally placed and those with them close together we have a third class, of which the horse, ox, and sheep are examples, where the eyes, though laterally placed, are situated so far forward that both may be brought to bear on an object.

When a horse directs both eyes to the front, as he does when attentively looking at an object, especially if it alarms him (see p. 584), he strongly converges his eyes, producing a double internal squint (Fig. 187). The eyes are rotated inwards and slightly upwards by the combined actions of the inferior oblique and internal rectus muscles; the pupils are nearly horizontal, and the pupillary opening brought so far to the front that the inner segments of the cornea and iris completely disappear beneath the inner canthus; the ears are erect and turned forward; the expression and attitude is one of intense attention. On reference to Fig. 188 it will be seen that the width between the eyes prevents an object situated directly to the front being seen as a single object, as it is in man, for the reason that the image falls on the temporal side of each retina—*i.e.*, on *opposite*, instead of on corresponding sides, as in man. There is no reason to think that the animal sees double, as a man under these conditions certainly would, and though we know that the horse has not binocular vision in the sense that this is assigned to man, the dog, and cat, it can with assurance be assumed that binocular vision is not absent, though it is limited in amount. A reference to Fig. 188 shows that objects situated away from the central line of the face can be seen with one eye only.

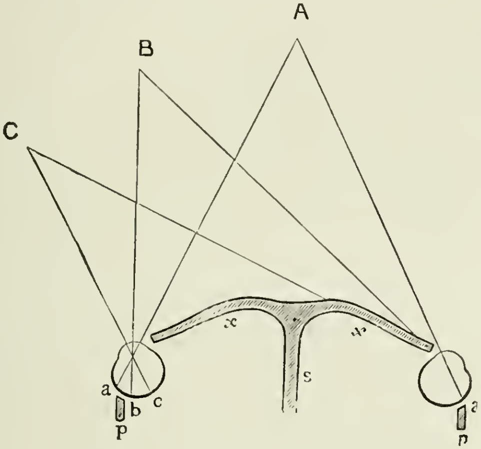

Fig. 188.—Diagram showing Horizontal Section of the Head passing through both Eyeballs, to illustrate Corresponding Points in the Retina of the Horse.

x, *x*, The frontal bones; *p*, *p*, portion of malar bone entering into the formation of the outer rim of the orbit; *s*, the nasal septum. Rays of light proceeding from A are seen by both eyes, being imprinted on the temporal side of each retina at *a*; rays from B are seen at *b* in the left eye, but are not seen with the right eye; in the same way rays from C are imprinted at *c* in the left eye, but cannot be seen with the right eye.

Monocular vision is vision with a single eye; it is not regarded as so quick nor so sure as binocular, and is found in animals which do not have to depend upon their own exertions, skill, and cunning for obtaining food. It affords a wide field of view, which is termed *panoramic*. Reference has been made (p. 583) to the fact that panoramic is also another term for peripheral vision in man, or vision occurring away from the macula. A man has panoramic vision extending over a field of at least 90 degrees, and very oblique rays may bring it up to 104 degrees, but as his acuteness of vision is limited to the macula, it is evident that only over a small fraction of the field is he able to see distinctly without moving the eyes. On the other hand, it is thought that in the herbivora acuteness of vision extends all over the large visual field of 180 degrees; such vision is termed *periscopic*, and indicates that the picture seen by the eye is sharp and distinct, as is a photograph up to the edge of the plate. In this sense the herbivora have both panoramic and periscopic vision.

There can be no doubt that in the herbivora the retina is sensitive as far forward as the ciliary processes, and this, with a horizontal pupil, allows of extremely oblique rays entering the eye, an impossibility with eyes set close together and a circular pupil. The extremely oblique rays are refracted at the cornea, and, travelling parallel and close to the iris, are then further refracted by the lens, so as to bring them on the retina behind the ciliary processes. It is also likely that the structure of the lens, which, as we have seen, is not homogeneous, but made up of layers of different refractive indices, assists in bringing to a focus on the retina oblique rays which would otherwise be indistinct.*

An animal employing monocular vision for a near object at its feet is unable to see it without lowering the head and turning it on one side in such a way as to bring the eye opposite to the object. This is well seen in the bird and in the horse. Incidentally it settles the question of the distance at which a horse views a near object when he can make his own adjustment; it may be taken at about 3 feet.

Stereoscopic Vision.—Though objects are imprinted flat on the retina, nevertheless they are seen in relief. Vision which furnishes a knowledge of depth—*i.e.*, perspective—is known as stereoscopic. It is acquired by education. Everything appears flat to an infant; in those cases of blindness from birth, where sight has subsequently been obtained by operation, a knowledge of shape has to be obtained by means of the sense of touch. This applies also to the lower animals. The fear of an object may be dispelled by allowing a horse to smell and examine it. The carelessness shown by some in jumping is corrected by a rap on the shins, and future judgment assisted by a fall. The optical condition necessary in the eye for stereoscopic vision, is that the object shall be seen from two slightly different standpoints, the right eye seeing more of its right side, the left eye more of its left side. When this is obtained, as it is by the interval between the eyes, a single image is secured, and solidity results.* The physiological conditions necessary are the same as for binocular vision, the impressions from the left half of each retina being conveyed to the left brain, and from the right half to the right brain. This is effected through the direct fibres (see p. 582), and animals possessing no direct fibres, such as fishes and birds, are said to have no stereoscopic vision.

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* 'Sight,' J. Le Conte, LL.D., 1883.

The domesticated herbivora have no stereoscopic vision in the sense of the above definition, any more than they have true binocular vision; nevertheless, it is undoubted that they have the power of seeing a single object with a pair of eyes, and of judging the three dimensions in space. Even the loss of one eye does not prevent a horse from being able to jump. It has been suggested that the wide base on which his eyes rest assists stereoscopic vision, and this is probable.

Recent work† on stereoscopic vision offers the best explanation of it yet put forward. The picture is received in the eye on a concave surface, which in this respect offers a great contrast to the sensitive flat plate of the photographer. This concave surface distorts the image. If a distorted image be examined by reflection in a concave mirror, the eye of the observer is not only unable to see any distortion, but the image is *seen in relief*. The concave sensitive plate of the eye by distorting an image, renders it undistorted and in relief when projected into space. This appears to explain stereoscopic vision in animals which have no parallel vision.

Theory of Vision.—The change which enables the vibrating ether to start a nerve impulse is unknown. Cutting or stimulating the optic nerve causes no pain, but produces a flash of light. It is known that electric changes occur in the eye not only with flashes of light, but with what has been termed 'flashes of darkness.' If an excised eye be suitably connected to a galvanometer, the eye being kept in the dark, an electrical change occurs when light is transmitted through the pupil, and there is a similar electrical change when the light is withdrawn. The sensitiveness of the eye to these reactions increases by its being kept in the dark.

A photo-chemical theory of vision has been proposed. It is

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* The student should test this on himself by looking at an object first with one eye and then the other without moving the head, and observing the slightly different pictures formed on the retina of each eye.

† J. L. Peach, *C. R. de la Soc. Biologie*, lxxxiii., No. 7, 1920.

suggested that under the influence of light waves chemical changes which give rise to a nerve impulse occur in the rods and cones. The presence of a red pigment in the retina, which becomes bleached by light, lends support to this theory. This pigment, known as **visual purple** (p. 584), is found in the external segments of the rods; the cones contain none. If the pigment be extracted and brought into solution, as it may through the action on it of bile salts, the coloured liquid thus obtained becomes bleached on exposure to light. Advantage is taken of this to obtain in the eye of a frog or rabbit, suitably prepared by being kept in the dark, a retinal photograph or *optogram* of an object, such as a window. The light bleaches the retinal purple, while the shadow of the framework comes out red. The colour having been discharged from the rods, regeneration occurs through the pigment of the retina; this penetrates between the rods and cones, and in due course the visual purple is restored to the rods. It has also been thought that light influences movement of the cones, producing shortening, whereas in the dark they lengthen.

It is important to remember that the decomposition of visual purple cannot wholly account for sight, for in man the area of acute vision, the fovea, is entirely without this pigment; it is also absent from the retina of such animals as the hen and pigeon, in both of which vision is acute.

An eye adapted to light, and therefore not adapted to darkness, is a condition with which all are familiar on passing from a light to a dark room; the vision improves by waiting in the dark, and it can be shown in man that the improvement does not occur over the cone area—viz., the fovea—but over the peripheral field, where the rods predominate. The explanation of the vision of night-seeing birds and animals probably lies in the function of the purple-coated rods, while acute daylight vision is probably the essential function of the non-pigmented cones. Neither the hen nor the pigeon, the habits of which are diurnal, can be regarded as possessed of eyes defective in acuteness of vision, yet, as we have seen, neither possesses visual purple. On the other hand, neither possesses vision suitable for night-time. In the bat visual purple has been found; in the owl it exists in abundance. It seems justifiable, therefore, to believe that the difference between eyes suited for daylight and those adapted to darkness largely depends on the visual purple, by which the irritability of the rods is increased in dim light, and vision is facilitated in illuminations of low intensity.

It is thought that vision results not only from incident, but also from reflected light, thus stimulating the sensitive elements a second time. It is safe to assume that this is the part played by the tapetum (p. 576), and that in its area the visual acuity is increased, especially in low degrees of light.

G. L. Johnson suggests that the tapetum may also be concerned with **Colour Vision.** He points out that in this structure the reds, yellows, and greens predominate; where blue or violet occurs in the tapetum it is tempered by the overlying retinal pigment, so that the fundus is mauve or greenish-blue. In dim light colours lose their distinction and appear uniform, with the exception of yellow and orange, and nocturnal animals have golden-yellow or golden green fundi. Birds, reptiles, and fishes have red, green, and yellow oil globules in the inner segments of the cones.

It is thought (Mottram and Edridge Green) that animals have no colour vision beyond red, green, and violet. Brown is a colour largely employed in animal colouration, owing to the ease with which it can be produced in metabolic processes; it is suggested that brown and green are indistinguishable by animals. Yet a horse makes no mistake when shown a bundle of green lucerne; he at once recognises that it is not hay, and shows his pleasure accordingly; similarly, he would certainly not mistake a parsnip for a carrot, an article of which he is inordinately fond. There was a well-known funeral contractor in London who at one time kept as many as 700 black Belgian horses in his stud. He found from experience that if he placed a horse of any other colour than black amongst them they became miserable and fretful. The experiment was made many times, but always with the same result.* It is evident that these horses were capable of recognising the difference in colour between brown and black. Why red should be so exciting to a bovine is not known, but his recognition of the colour is undoubted.

Divergence of the Optic Axis.—Reference has been made at pp. 574 and 597 to divergence of the eyeballs. The position of these in man and the monkey is practically parallel; in the cat the optic axis forms an angle of from 7 to 9 degrees with the middle line of the face; in dogs there is a good deal of variation due to breed. Johnson places it at from 15 to 25 degrees; he also gives for the pig, 33 to 35 degrees; horse, 40 degrees; ox and sheep, 50 to 52 degrees; hare, 85 degrees. We think the angular measurement given for the horse is too small; 45 degrees is about the angle for binocular vision, but for monocular its position varies between 50 and 60 degrees; if the eye be turned back to look out of the 'tail,' the angular measurement is about 75 degrees; the post-mortem position is about 65 degrees.

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* 'Horse World of London,' W. J. Gordon, 1893.

Field of Vision.—The angular measurement for man is generally given at 82·5 degrees, but H. Hartridge* allots him 104 degrees for each eye. In the hare the field is not less than 190 degrees for each eye; the fields overlap both in front and behind; the same occurs in the bird. This overlapping provides a visual field which completely encircles the head. In the horse the field of vision gives an angular measurement of 90 degrees on either side of the visual axis, so that with successive movements of the eye 180 degrees are covered. A large cornea, horizontal pupil, projecting eyes, and marked divergence of the optic axes secure a large field of vision.

Pathological.

Many of the diseases of the eye met with in man are found to occur in the lower animals, though not with the same frequency. They are of especial importance in those required for work where acute vision is necessary. An opacity of the cornea very seriously affects the value of a horse, quite apart from the defect in vision. The structures of the eye are so extremely delicate that very slight pathological change suffices to produce conditions which are incompatible with normal sight. A horse which is partially blind may be more dangerous for work than if the sight had been totally lost. **Injuries** to the eyes of horses are frequent, such as lacerated eyelids from projecting nails and hooks in the stable, injuries to the cornea and punctures of the eyeball caused in the hunting-field, and more commonly in the stable. The animal can afford no protection to its eyes other than by the use of the retractor muscle. As might be expected, the most serious injuries to the globe of the eye are produced by the smallest objects. A blow on the eye from a large object may not leave a mark on the eyeball, while a blow from a stick or the end of a lash may destroy vision. **Errors of refraction** have been discussed on p. 596, and need not be dealt with further; correcting lenses have been employed, but are never likely to prove popular. **Shying** is not necessarily due to defective vision, though there can be no doubt that both astigmatism and short sight are responsible for many cases. The most destructive eye disease is **Specific Ophthalmia** of the horse, an attack of which affects almost every tissue in the globe of the eye. Something resembling it has been observed in cattle in Europe and South Africa, but, speaking broadly, there is no eye disease in other animals or in man, which for intensity and destructiveness can approach it. When horses were taken less care of than they are at the present day, and the laws of health were less understood, the disease was rampant throughout Europe. In this country it is now relatively rare, but is still common both on the Continent of Europe and in North America. It was also seriously prevalent among the armies in the field, both during the Great War and the war in South Africa, 1899-1902. Operating through a series of attacks, each of which leaves the eye worse than before, it always leads to destruction of one or both eyes. **Cataract** is the most common internal disease of the eye in horses, and a serious cause of unsoundness. Contrary to what happens in cataract in the human subject, the lens may not become entirely opaque—in fact, total opacity is the least frequent condition met with. Spots of opacity, one or more, sometimes no larger than the head of a pin, and generally situated in the line of vision, represent the majority of cases of cataract. It has been shown by F. Valentin that the lens of the horse contains various lipoids (fat, fatty acids, and cholesterol) in solution, and that these may be deposited as amorphous particles. Cholesterol feeding in the dog produces deposits in various tissues of the eye, especially the cornea. There are some forms of cataract which escape detection when the eye is merely illuminated from the front, and can be seen only when the lens is illuminated from the back by means of the ophthalmoscopic mirror. In fact, no one can, without risk of error, declare an eye free from cataract without using the mirror of the ophthalmoscope. There are many cataracts concealed by the margin of the pupillary opening which become visible only when the eye is examined with this instrument.

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* *Journal of Physiology*, vol. liii., 1919.

A considerable amount of eye trouble occurs in animals as the result of infection from **specific diseases,** such as influenza in the horse or distemper in the dog.

Sympathetic Ophthalmia, so common in man after an injury, is not met with in the lower animals, certainly not in the horse. It is usual to consider the cause of the affection as due to inflammation extending along the direct fibres, and so affecting the opposite eye.

SECTION 2.

Smell.

The Olfactory Organ.—The nasal chambers are divided by a septum, and each chamber contains the turbinated bones. It has been observed that acuteness of smell is often associated with large and extremely convoluted turbinates. By the position of these bones the nasal passage may be divided into two channels: one which lies next the floor of the chamber, which, from its obvious communication, leads directly to the respiratory passages, and another channel which lies above it and leads to structures situated very high in the face and nose. One is known as the respiratory and the other as the olfactory passage. There are differences in the physical characters of the mucous membrane of the nasal chambers; that of the olfactory region differs from the membrane of the respiratory portion in being thicker and of a yellowish tint, and it is in this membrane that the fibres of the olfactory nerve are distributed. In all the herbivora and many other animals a peculiar organ is found in the nasal chambers known as the *organ of Jacobson*. In the horse it lies close to the septum, and consists of a tubular cartilaginous channel communicating anteriorly with the nasal chamber by means of an orifice. It is lined by mucous membrane and fibres of the olfactory nerve are distributed to it. It is an organ of smell. Both the respiratory and olfactory portions of the nasal chambers are supplied with sensation by the fifth pair of nerves. In the horse the nasal chambers are of extreme importance, inasmuch as he is the only animal we are called upon to deal with which is unable to breathe through the mouth; the majority of animals can breathe through both nose and mouth, but owing to the extreme length of the soft palate in the horse this is under ordinary circumstances impossible. So far as respiration is concerned the question of the nostrils has been dealt with (p. 117), but the arrangement of that portion devoted to the sense of smell has yet to be considered.

Olfactory Nervous Mechanism.—From the olfactory tracts in the brain the olfactory lobes are formed, which in some animals possess a well-marked cavity, in others only a canal. In the cavity some fluid is contained which communicates with the cerebro-spinal, and notably in the horse with that contained in the lateral ventricles. From the large olfactory bulbs non-medullated nerve-fibres are given off, which penetrate the cribriform plate of the ethmoid, and ramify over the mucous membrane, covering the upper portion of the septum, the superior turbinated bone, and the upper thirds of the superior and middle meatus.

These nerve-fibres terminate in olfactory sense organs, which are specialised nerve-cells, from the free end of which projects a tuft of hair-like processes, which are acted upon by olfactory stimuli. These nerves, if traced backwards into the brain, are found to terminate in globular bodies in the olfactory lobes, where they connect with the special cells of this region through the dendrites of the latter. The axons from the new cells are continued into the olfactory tracts of the brain by means of bundles of fibres, some of which terminate in the tract; others cross to the opposite side, to end in the grey matter of the hippocampal lobes; others pass to the hippocampal lobes of the same side. The sense of smell is located in this region, but the connections of the olfactory tract are numerous and incompletely known. The olfactory area is interesting developmentally, as being the first part of the brain to appear, showing the extraordinary importance of the sense of smell in animals very low in the scale. It is the only sensory tract in higher animals which passes directly to the cerebral cortex without going through the thalamus, and the cerebral hemispheres were derived from, and built upon, what in the primitive vertebrate was simply the receptive instrument for smell impressions (G. E. Smith). In animals possessing acute sense of smell the olfactory regions are highly developed (p. 535); in others, like man, where additional protective instincts have subsequently appeared, the sense of smell is not so acute, and the central representation accordingly greatly reduced. In animals where the sense of smell is lost, as in the porpoise and most fishes, the olfactory region is absent, while in others, like the shark, which is guided entirely by this sense, its development is extraordinary. In a shark 25 feet long the olfactory nerves spread out over an area of 12 to 13 square feet (Halliburton).

The Olfactory Stimulus.—Before an odour can affect the olfactory nerves it has to diffuse into the higher cavities of the nasal chambers, and from being gaseous it must become dissolved in the fluid which bathes these surfaces, for a dry olfactory surface is insensible to smell. All odorous substances must be soluble in water and in lipoid, as this material is contained in the olfactory cells. We have no idea of the nature of the particles which constitute an odour, but it is supposed that they act chemically on the hair cells. The odour of a body can be detected with greater accuracy by 'sniffing'; by this inspiratory act no time is lost in diffusion occurring between the respiratory and the olfactory region, as the odoriferous particles are forcibly drawn upwards. Colin performed a tracheotomy in horses, and tied the trachea above the incision. Under these conditions no air could pass up into the nasal chambers excepting by diffusion. Animals so treated were unable, with their eyes covered, to detect the presence of hay or oats. A stallion, however, under these conditions, was able to recognise a mare, though he failed to recognise food.

Olfactory Sensations.—There are certain odours which excite the olfactory organs more readily than others; thus flesh, blood, and offal have remarkably stimulating effects on the carnivora; whilst grass, grain, and vegetable products generally, stimulate the herbivora. The odour of blood or flesh is evidently repulsive to the herbivora, and may even cause nervousness and fright; there are exceptions to this, for horses have been known to eat meat with evident pleasure. The herbivora have a remarkably keen scent; antelopes and deer have the power of detecting the presence of an enemy a considerable distance away. All the herbivora are guided by smell in obtaining their food, for they cannot see what they are eating.

The acute sense of smell in the herbivora is a protective mechanism. Their sight, comparatively speaking, is not acute, certainly not nearly so keen as that of the animals by whom they are hunted. Horses are quite conscious of the presence of a lion, and exhibit great alarm and anxiety when one is about. The sense of smell is also popularly believed to afford instruction to animals in distinguishing poisonous from non-poisonous plants, and the organ of Jacobson was supposed by Cuvier to afford this protection. Smell, however, plays a very unimportant rôle in this connection. Cattle-poisoning as the result of grazing is common all over the world, and especially in South Africa. Experience is here the best master, and survivors may generally be left on a pasturage known to contain poisonous plants, for they have learnt to avoid them.

It is through the sense of smell that the male is attracted to the female during the 'œstrous' season, and not only can the odour of a female in this condition be detected at a considerable distance, but the smell is evidently most persistent. By the sense of smell animals have the power of recognising their own offspring; a cow which has lost her calf will yield milk for weeks to a 'dummy' clothed in the skin of the dead calf, and she can recognise the difference between her 'dummy' and that belonging to another cow. If the skin of a young animal—a kid, for instance—be dressed with an agent which disguises the body-smell, the mother is unable to recognise her young. The odour of food is readily recognised by the herbivora, though to the human senses all grains are equally free from any smell but that of the sack which contains them. Without tasting it, a horse will refuse a grain he is not familiar with. It is possible that everything and everybody has a distinctive odour—at least, it would appear to be so from the remarkable manner in which hounds will follow a scent, or a dog recognise his own master in the dark from amongst a crowd of other persons. In the case of hounds, the amount of odour required to stimulate the olfactory organ must be something too infinitesimal for expression.

The elevation of the upper lip in the horse is associated with the sense of smell. The stallion, on approaching a mare, exhibits this evidence of the pleasurable impression on his olfactory organs, but he does exactly the same after having had a draught of aloes poured down his throat, the bitterness of which he greatly resents.

The sense of smell rapidly becomes blunted—at any rate, in ourselves; any oppressive odour is always more marked when first detected. The writer has never satisfied himself that animals are conscious of an offensive odour. Garbage is evidently not offensive to a dog; horses certainly take no notice of the smell from putrefying bodies, though they refuse to pass them if visible, but that is only because they do not expect to see either men or horses in any other than an upright attitude.

SECTION 3.

Taste.

The sense of taste is largely, though not quite, dependent upon the sense of smell. There are certain substances which cannot be distinguished when the nose is closed; there are others which can be readily distinguished by the tongue alone. This has led to a **classification of taste** sensations, of which four kinds exist—viz., *sweet, bitter, acid,* and *salt*. Animals are certainly capable of distinguishing all of these. It is probable that each distinct taste affects a particular part of the tongue; in man it has been shown that the back part is sensitive to bitter tastes, the tip to sweet and saline tastes, the sides to acid tastes, while the middle portion of the tongue is insensitive to any taste. The *flavour* of a substance is not obtained by the sense of taste alone, but by the union of the senses of smell and taste. Without smell, taste would be nearly impossible.

Tongue Papillæ.—The papillæ of the tongue are spoken of as *filiform, fungiform, circumvallate,* and *foliate*. The *filiform* occur over the upper surface of the organ, and in the ox impart to it its characteristic roughness. The *fungiform* papillæ in the horse exist principally on the lateral parts of the tongue; the *vallate* are found far back on the dorsum, and are only two or three in number in the horse, twenty or thirty in the ox. The *foliate* papillæ are characteristically present in the horse, forming a large projection in front of the pillars of the soft palate. There are none in the ox, but they are very markedly present in the rabbit. The filiform are in function chiefly tactile, the fungiform, circumvallate, and foliate papillæ, are associated with the sense of taste, and in their structures are found the special nerve organs of taste, known as **taste buds,** bulbs, or taste goblets. These are balloon or barrel shaped bodies, the walls of which are formed of elongated cells resembling the staves of a barrel. This structure is open top and bottom; the nerve-fibrils enter below, while at the outer free end is the gustatory pore, or opening into the interior of the body of the bulb by which fluid finds its way in. The interior of the goblet or bulb is filled with two kinds of cell closely similar to those of the olfactory organ. Of these, some are of a cylindrical shape, and are probably sustentacular. The others are rod-shaped, and have at their outer ends a hair-like process which projects at the pore. It appears to be essential to taste that fluid should readily find its way into the pore, and as a provision to insure this the papillæ containing the buds are situated close to glands. M'Kendrick states that in a single circumvallate papilla of the ox 1,760 taste goblets have been counted. The goblet cells are not strictly limited to the tongue, but have been found in the palate, epiglottis, and even in the larynx.

Nerves of Taste.—It will be remembered (p. 555) that the posterior third of the tongue is provided with sensation by the glosso-pharyngeal nerve, the anterior two-thirds of the organ by the lingual branch of the fifth pair. These two nerves, besides endowing the tongue with sensation, are also concerned in carrying those impulses connected with the sense of taste. The cortical centre for taste is not definitely known, but is considered to lie close to that of the olfactory sense in the hippocampal lobe. It is believed that the taste-fibres in the lingual branch of the fifth pair are furnished by the chorda tympani of the seventh pair after the latter leave the middle ear. Stimulation of these fibres arouses a sense of taste; this not only places their function beyond doubt, but also proves that, apart from the stimulation at the periphery, there is a specific taste reaction in the brain. The fibres of the fifth pair are not, however, connected with taste bulbs, for none are found over the area of their distribution. The taste bulbs are the essential nerve terminations of the glosso-pharyngeal nerve, and if this nerve be cut the bulbs degenerate. Motor power to the tongue is furnished by the hypoglossal or twelfth pair; section of these nerves prevents an animal from masticating its food, the organ hanging helplessly from the mouth and receiving injury from the incisor teeth.

It is necessary for the purpose of taste that the substance should be dissolved; this is one of the functions of saliva, and experiments on herbivora show that taste produces an abundant secretion from the submaxillary and sublingual glands, though not from the parotid.

SECTION 4.

The Cutaneous and Internal Sensations.

The sensations imparted from the surface of the body to the animal are not of one character only; touch is different from heat, cold is something apart from pain. These four sensations of *pressure* or *touch, heat, cold,* and *pain,* make up the complex, combined or uncombined, which composes the cutaneous senses (p. 528). It is easy to realise the remarkably sensitive nature of the entire surface of the body. There is no part, excepting the horn of the feet or head, which does not give evidence of pain on being cut; there is no part, including the feet and horns, which is unconscious of touch or pressure. This sensory envelope is in the main protective, but it serves many other functions; some of these we have already studied under Respiration, Secretion, and Animal Heat; some have been referred to under the head of Muscle Tonus, on which more remains to be said.

There are also afferent impulses proceeding from the skin which indicate to an animal the position of its limbs, which direct its muscular efforts, enable it to judge of weight and resistance, and, in conjunction with afferent impulses from muscles, initiate the changes which lead up to a muscular contraction. With none of these are we at present concerned, but only with those afferent impulses of common sensibility and pain proceeding from the skin to the central sense-organs, where their nature and character can alone be realised and distinguished, though the sensation is referred to the stimulated surface, and not felt in the brain.

In the matter of sensibility there is a great contrast between the surface of the skin and all that lies beneath it. Under normal conditions muscles, bones, and tendons exhibit no ordinary sensibility; even when aroused by disease they are still devoid of touch, heat, and cold sensations, though pain may be felt acutely. It will be remembered (p. 564) that the thoracic and abdominal viscera are normally devoid of ordinary sensibility.

Experiments made by Head and Rivers have shown that there are two sets of sensory skin-fibres—a deep and a superficial. The former, *protopathic,* convey sensations of pain, and of marked heat and cold; the latter, *epicritic,* convey sensations of touch, and small differences of heat and cold. Touch sensations are divided into those of tactile localisation and tactile discrimination; these are conveyed by separate nerve-fibres—in fact, distinct fibres exist for all the cutaneous senses; those conveying pain do not transmit cold, and those transmitting cold do not convey heat. It is remarkable that touch, heat, cold, and pain senses are distributed over the surface of the skin in spots or dots. There are spots which are responsive to pressure; others to warmth; others, again, to coldness; and on suitable stimulation others feel pain. Maps showing the distribution of these four surface senses have been prepared in man, in whom alone their differentiation is possible. There is no reason to think that the same principle of distribution does not hold good for the lower animals.

Temperature Sense.—Cold spots are more widely distributed than warm, which suggests that it is more necessary that the body should be made acquainted with the fact that it is cold than that it is hot. The feeling of warmth or cold depends upon the temperature of the skin, and not upon that of the body.

Light Pressure Sense.—The distribution of the spots is wider than of those of the temperature sense. The special nerve-endings connected with pressure are found in a ring around the hair follicles, in which position they are obviously most favourably situated for stimulation through the hair itself. In the hairless parts of the skin and muzzle special tactile corpuscles are found, and in the horse special nerve-endings exist in the foot associated with tactile sensibility. Tactile sensations play a very important part in the lives of animals. In the lips and muzzle, which correspond to the fingers of the biped, the touch organs proper are located (p. 308); these parts are endowed with exquisite sensibility, which enables the animal to be kept acquainted with the nature of its surroundings and the character of its food. The long feelers or hairs growing from the muzzle, face, and brow of the horse are in connection with nerves in the skin, and are valuable for tactile and consequently protective purposes. The 'cat hairs' on the general surface of the body are doubtless for the same purpose. The tactile sensibility of the foot, by informing the animal of the character of the ground it is travelling over, is useful, though not absolutely essential, in locomotion; nor is the tactile sensibility in the foot of the horse absolutely essential to its safety in progression, as is clearly proved by the results of plantar neurectomy.

Pain Sense.—This is the most widely distributed of the cutaneous senses. It is distributed in spots probably supplied by special fibres, though no special nerve-endings have been determined. Pain confined to the surface of the body can be readily located, but the localisation of interior pain is difficult; that of colic, for example, is referred to the abdominal wall. It is supposed that the explanation of the difficulty in localising interior pain is that the segment of the spinal cord supplying the affected organ refers the pain to the skin region of the same spinal segment instead of to the organ (p. 564). Painful sensations are of various characters—hence such terms as 'stabbing,' 'boring,' 'burning,' 'throbbing,' etc., to express the impression imparted. It is presumed that amongst the lower animals these different qualities of pain exist; it is quite certain, for instance, that the pain exhibited by a horse during an attack of colic is very different from that shown when pus is forming in the foot. Of the nature of pain nothing is known; for its seat see p. 511.

Muscle, Motorial, or Kinæsthetic Sense.

The term 'muscle sense,' or *deep pressure sense*. has been employed to describe several allied, though quite distinct, conditions to which the muscles directly or indirectly contribute. It covers such questions as a knowledge of the existence of muscles and of their position, the position of the limbs at rest and in motion, the proper and orderly contraction of muscles, and of the correct grouping of sets of muscles—viz., muscular co-ordination—both for locomotion and for equilibrium. It goes further: it deals with weight and the resistance offered in muscular contractions, and in conjunction with touch and sight it contributes to the formation of spatial conceptions. To many it has appeared that the grouping of this set of complex functions under the term 'muscle sense' is liable to prove misleading, for there is no evidence that in all cases the muscles play a predominant part in the various phenomena; in consequence, the term **motorial** or **kinæsthetic sense** is considered a more suitable designation.

Sherrington has shown that muscles receive a rich supply of afferent nerves, one-half to one-third of the nerves in muscle being of this nature. These sensory fibres terminate in special nerve-endings in the muscle or its tendon. These endings are known as **muscle spindles** (p. 423); they are believed to be activated by variations in the tension of the muscles. The proof that these spindles are sensory in nature is afforded by the fact that when the inferior roots of the spinal cord are divided no degeneration of them occurs. It is through these fibres, which enter the cord by the dorsal roots and travel both to the cerebrum and cerebellum, that the brain is made acquainted with the condition of the muscles. The cerebellum, through its connection with the semicircular canals of the internal ear, enables a judgment to be formed of the position of the body in space, and of its relationships to its surroundings (p. 628). These are communicated to the cerebrum, from which impulses pass from the centre representing the muscles to the muscles themselves. It would appear that centres must exist in the cord by which at least part of this work is carried out, for it has been shown (p. 482) that after the cord has been divided in the dog, and sufficient time has elapsed, muscular co-ordination is re-established, though no communication with the brain is possible. There are other reasons which have also been mentioned which suggest that the cord of the lower animals is capable of automatic activity in the matter of muscular movements, being stimulated by the constant inpouring of sensory impulses through the muscle afferents.

Deep pressure sensibility, such as arises from joints, and the sensory impressions arising in the skin and subcutaneous tissues of joints, are intimately concerned in the kinæsthetic sense. It is probable that this deep sensibility is particularly employed in determining weight and resistance, and it would appear to be well developed in draught-horses. The horse employed in 'shunting' knows in a second the amount of effort required to start truck-loads of varying weight. This information is transmitted through the skin under the collar and over the large joints, especially the shoulder, hip, and stifle.

The importance of 'muscle sense' in provoking a muscular contraction is shown by the pseudo-paralysis which follows division of the sensory nerves (p. 504). This operation causes no loss of power, but it cuts off all afferent impressions from the muscles of the part; the dog drags his legs, the arm of the monkey hangs helplessly, in spite of the fact that in neither case have the motor mechanisms been interfered with. The same is seen in the horse on dividing the superior maxillary branch of the fifth nerve; the animal is unable to use his lips as a prehensile organ, though they possess their full power (see p. 554).

Judgment of distance, the relationship of space, and the muscular co-ordination connected with equilibrium, are indefinably mixed up with muscle sense, vision, and the internal ear. The extraordinary judgment shown by horses in jumping, both as to height and distance, is mediated through this channel. Some animals never acquire it, are clumsy, and make but little effort to rise, or, if tired, none whatever; others are willing, but their judgment is defective, and the muscles are directed to perform unnecessarily powerful contractions; a third group, confident in their powers and judgment, and unwilling to do more than is necessary, leave themselves such a fine margin of safety that it requires a fall to chasten their pride. Muscle sensation is very evident in the tired animal, and fatigue is probably the only condition, apart from lameness, in which a horse is conscious of possessing limbs.

Muscle sense has been referred to in the chapters on the muscular system (p. 423), nervous system (pp. 491, 504, 517, 528), and will be again met with in dealing with locomotion.

Hunger.

The sensation of hunger is referred to the stomach. It has been supposed that it is excited by the approximation of the walls of the organ, but animals may exhibit hunger at a time when the stomach contains food—for instance, the horse and the rabbit. Nothing is known of the nervous mechanism connected with this condition. It is one of the senses under the control of a lowly organised part of the brain, for a dog without its cerebrum shows the usual signs, though obviously this hunger cannot be associated with any conscious knowledge of want. The length of time animals will withstand starvation is dealt with at p. 393. A horse in good condition has been known to live thirty days, provided water be given; but an animal in poor condition to start with has died in half that time. The remarkable period during which sheep have lived without food has been mentioned at p. 393, and a similar endurance has been recorded in the pig;* the animal was buried for sixty days in a landslip, and was recovered alive, having lost in that time 120 pounds in weight. It is not known why eating gives practically *immediate* relief to all the symptoms of hunger, for it is obvious that the food ingested can be of no use until absorption has commenced

Thirst.

Very little is known of the subject of thirst—not even why the sensation is referred to the pharynx. It has been supposed that the glosso-pharyngeal nerve has special nerve-endings in the pharynx, which are stimulated when the water content of the body falls below a certain point; for if the palate be moistened thirst is allayed, while filling the stomach with water through a fistula does not at once control the desire for fluid. If a horse be 'sham watered'—viz., with a fistula in the œsophagus—he leaves off drinking, after a few swallows, as if satisfied, and then starts again as the pharynx gets dry (Colin).

There is a constant loss of water occurring in the body fluid through respiration and the various secretions, such as sweat, urine, milk, and digestive juices. Some of the fluid of the latter may be reabsorbed; especially is this likely to occur in the case of such bulky secretions as saliva in the herbivora. The requirements of an animal for water are constant, though varying with the season and the nature of the food. In summer the loss by sweat in working horses, and the extra transpiration by the air-passages, all have to be made good. Animals receiving dry food require more water than those on green herbage. According to Colin's researches, 4 kilogrammes (8·8 pounds) of hay require 16 kilogrammes (35·2 pounds) of saliva, and the fluid for this has to be drawn from the blood. When ' roots ' form a portion of the daily diet, the amount of water consumed becomes considerably reduced. So much is this the case that sheep fed on roots and succulent food are not watered; and the rabbit receiving succulent food does not drink. The assumption that neither of these animals requires water is at once disproved by placing them on a diet of dry food. Purging, hæmorrhage, and diabetes, prove severe sources of water loss to the tissues.

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* Martell, *Transactions of the Linnean Society*, vol. ix.

Thirst is badly borne by animals, certainly by the herbivora. With horses the capacity for work falls off considerably, and as the fluid contents of the digestive canal and tissues is drawn upon the abdominal wall contracts, and the animal wears a pinched and anxious look. Under these conditions in war, horses have been known, on obtaining access to water, to drink until they died, presumably from rupture of the intestines.

The ordinary exhibition of thirst in stabled animals is at once recognised by the trained eye. The horse that pricks his ears and gazes intently when he hears the sound of a bucket, and the peculiar motions of the mouth of the thirsty horse at the sight of water, are indications as unmistakable as speech.

Deprivation of fluid is productive of intense suffering. Hunger may be taken philosophically, but not thirst; the latter extinguishes life in a few days, the former in a few weeks. So essential, indeed, is the regular renewal of fluid that the sick animal, though turning from food with disgust, never fails, but in one disease, to consume fluid; during acute abdominal pain a horse will not drink, yet the leathery dryness of the mouth suggests thirst.

SECTION 5.

Hearing.

The Nature of Sound.—The vibrations which produce sound are transmitted by air, solids, and liquids in the form of waves. Through air, sound is transmitted by a succession of condensations and rarefactions of the air, due to its elasticity and density. The particles in the air oscillating to and fro are sometimes crowded together, at others widely distributed. The sound-waves travel longitudinally at a relatively slow rate—about 1,200 feet per second; the length of the waves varies from a fraction of an inch to sixty or more feet. The evidence that sound is transmitted by particles in the air is shown by the fact that it cannot be produced *in vacuo*.

In comparing one sound with another we are conscious of only three possible differences between them: they may differ in loudness, pitch, and quality. Of these, loudness is dependent on the *magnitude* of the to-and-fro motion of the vibrating particles whose movements transmit the sound; a loud sound means a large wave. Pitch, on the other hand, depends on the *frequency* of the vibrations, a high note implying rapid vibrations, or a shorter wave-length. Sounds may be simple or compound. The vibrations of a tuning-fork give rise to a typically simple sound of varying loudness or pitch, but possessing little quality. Most vibrating bodies do not give rise merely to such simple vibrations, but set up a variable series of different wave-lengths along with their fundamental simple vibration. Thus, most sounds consist of a fundamental tone, accompanied by more or less of these other tones—the *partial tones, overtones,* or *harmonics,* as they are termed. The quality of a sound depends upon these harmonics; where they are absent the tone is thin, where they are present they give richness, and confer on tone that 'character' which enables us to recognise one musical instrument from another by the mere sound it emits. Those sounds which are grouped under the general term of 'musical' result from the regularity of their causative vibrations, and the definiteness in wave-length of the latter. *Noise* is essentially the result of the absence of this regularity and definiteness. There is usually no difficulty in discriminating noise from musical sounds, but the one may merge into the other, as in the case of the noise of street traffic when near to it, and the musical humming tone it produces when heard from a distance. From observations on the human subject it has been ascertained that the smallest number of vibrations audible is about thirty per second, whilst the average human ear can recognise up to 30,000 vibrations per second. It is undoubted that some animals can recognise a smaller number of vibrations than thirty per second. Galton has shown that the cat is capable of recognising sounds inaudible to the human ear.

External Ear.—The vibrations of sound are collected by the external ear, which is formed of a movable funnel-shaped piece of cartilage of the yellow elastic type. Its mobility is greatest in animals which are preyed upon, such as the herbivora, and which in consequence require to collect sound-waves from every point. The ears differ in shape in every animal, and there are marked differences among animals of the same species.

The movements of the ears give evidence of what is passing through the mind of an animal; this observation is as old as Pliny. In the horse, which may be taken as typical, they are turned firmly to the front and closely pricked—*i.e.*, the points approximated—when he is attentive, whether this attention be devoted to something he is alarmed at or pleased with. They are laid back on the poll in sourness of temper, vice, anger, or during rough play unattended by vice. This is a protective mechanism; when horses fight with their teeth, the neck and ears are the parts which are aimed at; the mane is intended to protect the neck; the ears have to take care of themselves, being kept as far as possible flat on the poll.* The ears are moved rapidly to and fro when the horse is anxious, either from impending danger or other cause; one ear carried forward and the other backward, or both turned backward but kept firmly erect, is considered the sign of a willing determined worker. The carriage of one ear forward and the other backward suggests that the animal is able to appreciate sound from opposite points of the compass. Drooping ears are indicative of exhaustion, and when permanent are associated with age or natural flabbiness. Cattle, sheep, and goats never draw back the ears. It is rather remarkable that the expression of the mind in many animals should be conveyed through opposite poles of the body—*i.e.*, the ears and tail. In dog, cat, and horse movements of these parts tell each its own distinctive story. Wagging the tail, which shows pleasure in the dog, indicates irritation in the cat, and the vice of kicking in the horse.

The *conchial* or *auricular* cartilage forms the funnel which collects the sound-waves; it is pivoted upon another and much smaller cartilage, the *annual*, over which it slides as a telescope over the joint, while the annual cartilage is similarly fitted over the auditory canal of the petrous temporal bone; a few elastic bands hold these peculiar joints in apposition. The auricular cartilage is largest above, gradually contracting until it approaches the annular, when a sudden reduction in size occurs. The ear is capable of rotation through an angle of 180 degrees, and this remarkable mobility is secured by the cartilaginous joints above described, without the intervention of a synovial apparatus; but at the base of the conchial cartilage is a large pad of fat, which never undergoes absorption, and on this cushion easy rotation is assured.

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* The ears are also drawn back and laid on the poll in cases of violent death—for example, by shooting.

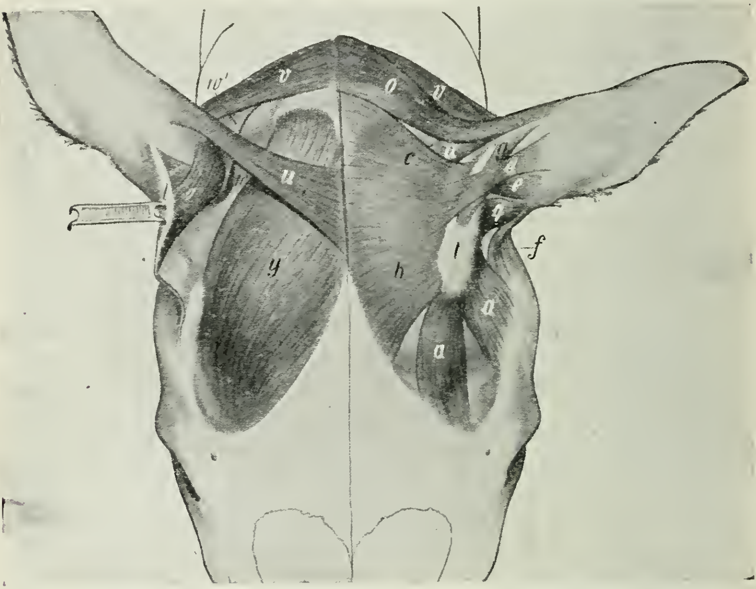

Fig. 189.—Muscles of External Ear of Horse (Sisson-Ellenberger-Baum).

On the right side the superficial muscles and the scutiform cartilage have been removed to display the deeper muscles. *a*, *a'*, *b*, *c*, Various branches of the scutularis muscle; *d*, *e*, *q*, *f*, anterior auricular group; *g*, *u*, superior auricular muscles; *o*, *v*, *w*, posterior auricular muscles; *x*, *x'*, deep auricular muscles; *y*, temporalis muscle; *t*, scutiform cartilage.

The skin covering the concha is fine and directly adherent to the upper two-thirds of the underlying cartilage; internally it lines both the conchial and annular cartilages so intimately that it largely assists in their union. The part at the entrance to the ear is provided with long woolly hair to prevent the ingress of foreign bodies; this hair becomes finer as the depth of the tube is approached, and finally is replaced by glands which secrete *cerumen* or ear-wax. At one point the conchial cartilage is attached to the guttural pouch; these organs will be dealt with presently.

According to Sisson, there are sixteen extrinsic muscles of the ear, and three intrinsic, the latter being small and unimportant; we shall confine our notice to the extrinsic muscles. In connection with some of these, the anterior group, there exists a most peculiar anatomical arrangement in the form of a floating cartilage, the *scutiform ;* from this certain muscles originate, while others hold it in place, and alter its position to agree with the direction in which the group attached to it have to act. The scutiform cartilage is a concave plate which lies on the temporalis muscle; there is nothing to keep it in position but the muscles which anchor it. It may be pulled inwards, downwards, or outwards, each change in position altering the direction of the pull of the muscles which arise from it in their action on the conchial cartilage (see Fig. 189).

The movement of the external ear through an angle of 180 degrees indicates that there is a group of rotating muscles; to enable the ears to point to the front there is a group of adductor muscles; in order that these points may approximate other muscles are employed; to enable the ears to point backwards a distinct group of muscles comes into play, while other muscles pull the ears down and lay them parallel to the poll. It is obvious that the muscular movements are very complex, necessitating perfect co-ordination, fine adjustment, and alterations in the position of the floating cartilage, in order to change the direction of the pull of those muscles which arise from it. There is no other part of the body where a similar physiological arrangement exists.

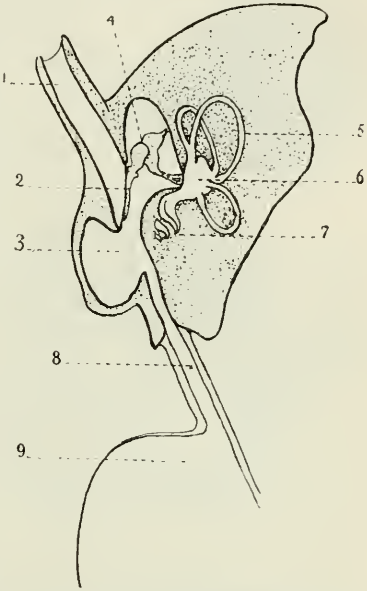

Fig. 190.—Diagrammatic Section through the Petrous Temporal Bone.

1, External auditory canal; 2, membrana tympani; 3, middle ear, containing the chain of small bones (4) which connect the ear drum with the internal ear; 5, one of the semicircular canals; 6, the vestibule; 7, a portion of the cochlea; 8, the Eustachian tube, which enters the middle ear; 9, portion of the guttural pouch, a diverticulum of the Eustachian tube.

The Guttural Pouches.—These remarkable air sacs are confined to the equidæ. Placed beneath the base of the skull and atlas and above the pharynx, they communicate with the outside air by means of the **Eustachian tube** (Fig. 190). As the Eustachian tube communicates with the middle ear, and passes completely through the guttural pouch as an open canal, it is not unreasonable to believe that the pouches are concerned with the sense of hearing. In man acuteness of hearing is enhanced by listening with an open mouth. The fact that the horse cannot breathe through the mouth may explain the presence of these large air sacs for the supply of the needful amount of air to the middle ear. This view is supported by the fact that the pouch is attached to the conchial cartilage, and when the ears are carried forward, as in attentive listening, the walls of the guttural pouch are rendered tenser. Air enters the guttural pouch during swallowing, and also during expiration; in the latter respect it resembles the facial sinuses. The use of the Eustachian tube is to convey air to the middle ear, and so equalise the pressure on both sides of the tympanum.

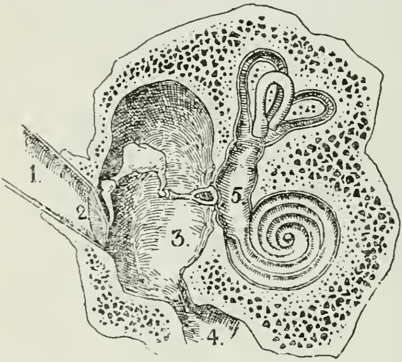

Fig. 191.—Diagrammatic Section of the Horse's Ear.

1, External auditory canal; 2, the membrana tympani; 3, chain of bones across the middle ear; 4, the Eustachian tube; 5, the internal ear; the number is on the vestibule, above which may be seen the semicircular canals, while below is the cochlea.

Structure of the Ear.—At one end of the external auditory canal is a piece of membrane stretched completely across it, known as the *Membrana Tympani ;* it separates the external from the middle ear (Fig. 191). The *Middle Ear* is on the inner side of the membrana tympani; it consists of a cavity containing a chain of very small bones, which stretch like a bridge across the space from the membrana tympani to the third or internal ear. The middle ear, like the external, is in communication with the air by means of the passage known as the *Eustachian tube*, which opens into the pharynx. The membrana tympani has, therefore, air on both sides of it, the object of which is to insure that the atmospheric pressure on both sides is equal, and so permit its free swing. The air ordinarily finds its way into the Eustachian tube during the act of swallowing, and it is conveyed to the guttural pouches by the same channel. The *Membrana Tympani* is concave towards the external ear; in the middle ear the handle of the *malleus* is fixed to the central bulging part of it, and as this bone articulates with the *incus*, and the latter with the *stapes*, any alteration in the shape of the drumhead, such as is produced by the vibrations of sound, causes the bridge of bones to move; their movement is further assisted by two small muscles which are attached to them.

The *Internal Ear*, known as the *labyrinth* (Fig. 192), is composed of the *semicircular canals*, the *vestibule*, and the *cochlea;* these are contained in a solid piece of bone in which two small foramina or windows exist, one known as the *fenestra ovalis*, the other the *fenestra rotunda;* the base of the stapes or third bone of the ear is attached to the membrane which covers the fenestra ovalis.

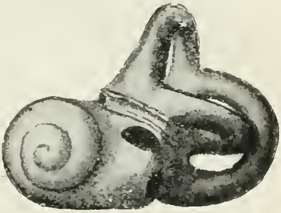

FIG. 192.—THE LABYRINTH (EDMUNDS).

The semicircular canals are to the right, the cochlea to the left; both windows may be seen, the *fenestra rotunda* being the lowermost. The groove across the body of the organ lodges the auditory nerve. The figure is enlarged.

All three parts of the *labyrinth* communicate, but it is quite certain that all three do not take an equally active part in hearing. The cochlea alone is the essential organ of hearing. The whole of the labyrinth is lined by a membrane containing a fluid known as the *peri-lymph;* this peri-lymph has free access to all parts of the inner ear. Within this membrane is a membranous labyrinth, the counterpart of the semicircular canals and vestibule, and this also contains fluid known as *endo-lymph*.

Two windows exist in the bony labyrinth. The base of the stapes lies over one of them, and between the stapes and the peri-lymph is the membrane which lines the internal ear. Every movement of the membrana tympani causes the bony bridge to oscillate, and every oscillation of this thrusts the stapes against the membranous window, and so sets up oscillations in the peri-lymph which are transmitted throughout the internal ear.

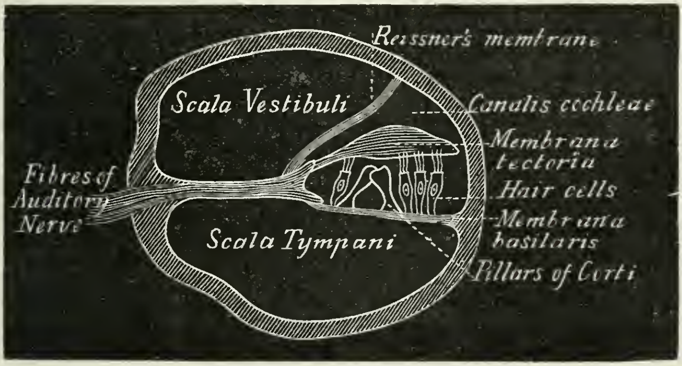

FIG. 193.—DIAGRAMMATIC TRANSVERSE SECTION OF A TURN OF THE COCHLEA.

The *cochlea* resembles in appearance the shell of a snail, its interior being divided into three spiral channels, which wind their way from base to apex like a circular staircase. The number of twists in the cochlea is two and a half; the axis around which these wind is composed of soft bone having canals up which the auditory nerve travels. If a spiral of the cochlea be cut across (Fig. 193), the three canals it contains are seen. These are divided by septa; one septum, known as the *lamina spiralis*, separates the upper canal, or *scala vestibuli*, from the lower one, or *scala tympani*. The third, or middle canal, is of a triangular shape, and called the *cochlear canal;* it contains the essential organs of hearing, and lies between and to the outside of the other two. The roof of the cochlear canal is formed by a piece of tissue known as the *membrane of Reissner*, while its floor, on which is situated the essential organs of hearing, or *organ of Corti*, is formed by the *membrana basilaris*, which connects the outer wall of the cochlea to the lamina spiralis; a cover to the organ of Corti is formed by the *membrana tectoria*. The cochlear canal is the continuation of the membranous labyrinth. The upper passage of the cochlea—*i.e.*, the scala vestibuli—is continuous with the lymphatic peri-lymph space of the vestibule, whilst the scala tympani, or lower passage, ends at the base of the cochlea in a blind extremity in which is a membranous window, the fenestra rotunda, which separates the scala tympani from the cavity of the membrana tympani. The cochlear canal terminates suddenly at the summit of the cochlea, and at this point the two scalæ, which in their windings have been decreasing in size from base to apex, meet and communicate by a small opening, the *helicotrema*, and the fluid of the one is thus in connection with that of the other.

Organ of Corti.—This consists of a triangular-shaped tunnel (Fig. 193), the base of which rests on the basilar membrane; the tunnel is composed of certain rods arranged side by side, inclined from both sides towards each other, and meeting superiorly like an inverted **V**. At this point the rods known as the rods or pillars of Corti, fit into each other in a peculiar manner, and by means of a membrane (not shown in the diagram), the *membrana reticularis* are connected with the cells containing the terminations of the auditory nerve. Flanking either side of the rods are certain cells of two distinct kinds; those nearest to the pillars are somewhat flask-shaped, and, having hairs growing from their summits, are spoken of as the *inner* and *outer hair cells*. The hairs on these cells are stiff and pass into holes in the *membrana tectoria*. External to the outer hair cells are some tall conical cells known as *Hensen's cells*. The auditory nerve ascends the axis of the cochlea, giving off branches which in their passage ramify over the lamina spiralis, at the outer edge of which the above-described organ of Corti exists; having reached this, the fibres lose their medulla, and the naked axis cylinders pass into the cells flanking the triangular tunnel, some fibres crossing the tunnel to reach the cells on the opposite side. How the nerve terminates in the hair cells—for it is to these that it is distributed—is unknown, but that the hair cells are the organs of hearing is undoubted; Hensen's cells are probably only of a nutritive nature, and unconnected with auditory impulses.

Auditory Sensations.—Any analysis of these is hardly necessary in a work dealing with the lower animals; we have no direct evidence that they understand or appreciate the difference between music and noise; a dog will howl at the one as readily as at the other. At the same time it is certain that animals can learn to recognise sounds and associate them with certain ideas, as, for instance, working instructions for either horse or dog, words of command, trumpet calls, or the master's voice. Every dog owner believes that his animal understands all that is said to it; certainly, in the case of the sheep-dog it is astonishing what he is capable of comprehending. Further, we have undoubted evidence that sounds which are so feeble as not to affect the human ear are readily perceived by some animals, so that the acuteness of their sensations is greater than that of our own.

When the vibrations of the air molecules reach the membrana tympani, the drum moves in and out, and so sets in motion the chain of bones in the middle ear. This chain acts as a bent lever, whereby its movements, though reduced in amplitude, are rendered more intense, so that the stapes through the fenestra ovalis imparts a push to the peri-lymph of the labyrinth. This impulse is transmitted through the fluid of the vestibule, and thence into the scala vestibuli of the cochlea; it then ascends the spiral staircase and sets in motion the membrane of Reissner, which causes the lymph in the cochlear canal to vibrate; these vibrations reach the summit of the cochlea and enter the scala tympani through the helicotrema. The lymph in this canal is set in motion, with the result that the basilar membrane on which the organ of Corti rests is also affected, and ultimately the vibrations reach the fenestra rotunda, which in turn is pushed out. Every push inwards of the fenestra ovalis causes, therefore, a push outwards of the fenestra rotunda.

The organ of Corti is suspended in fluid, and, as we have seen, rests on the basilar membrane; this membrane increases in width from the base to the apex of the cochlea; it is composed of fibres or strings, each string, it is supposed, being connected with a branch of the auditory nerve. According to the theory of Helmholtz, the basilar membrane vibrates sympathetically when the movements of the fluid surrounding it correspond to its own period of vibration, in precisely the same way that a tuning-fork or the strings of a piano vibrate to their own notes from sounds in their vicinity, and to no others.

As the strings in the basilar membrane get longer and longer from the base to the apex of the cochlea, and as these are some 24,000 in number, it is assumed that ample provision is made for the analysis of sound, from the highest to the lowest notes, each note being picked out by sympathetic vibrations of the fibres concerned, and then transmitted to the brain by their branches of the auditory nerve. The organ of Corti is responsible for bringing the vibrations of the fibres of the basilar membrane into communication with the nerve-endings by means of a rocking motion imparted to it by the vibrations of the basilar membrane, the result being that the hair cells are moved from side to side in the pores in which they lie, and so stimulated.

The most recent theory of hearing is that propounded by Wrightson.* He rejects the theory of Helmholtz with its basilar strings, each having an individual rate of vibration, and states that the basilar membrane vibrates over its entire extent as the result of the sound-waves causing fluctuations in fluid pressure within the ear; these fluctuations produce a rocking movement of the organ of Corti, and consequently to-and-fro movements of the hair cells; the impulses thus set up are then conveyed to the brain for analysis. The differences in the rival theories are that Wrightson believes that the whole of the basilar membrane vibrates—in consequence, every hair cell being stimulated—and that the analysis of sound does not take place in the cochlea, but in the brain. There are, however, difficulties of a physical character connected with this theory which require explanation before that of Helmholtz can be regarded as displaced.

Semicircular Canals and Vestibule.

We have seen elsewhere (pp. 515, 549) that the eighth pair of cranial nerves consists of two roots, dorsal and ventral, both distributed to the internal ear, but both are not concerned in the sense of hearing. The dorsal root alone is distributed to the cochlea; the ventral root passes to the vestibule and semicircular canals. In consequence, the roots have been distinguished as the cochlear and vestibular divisions of the auditory nerve. The cochlear division is exclusively devoted to the sense of hearing, the vestibular division to the function of maintaining the equilibrium of the body. The vestibular nerve is connected with the cerebellum, but not directly with the cerebrum.

The **Semicircular Canals** are three ring-like structures lodged in the petrous temporal bone; their positions are described as superior, posterior, and external. They are so arranged that their three planes are placed at right angles to each other, two being vertical and one horizontal, thus corresponding to the three dimensions of space (see Fig. 194). Their position in the petrous temporal bone is shown in Fig. 190.

The semicircular canals, together with the *vestibule,* constitute what are known as **position receptors**—that is to say, mechanisms which inform the animal of the position of its body relative to gravity, or of the direction in which its body is moving. They are not the only position receptors; it is obvious that the eye assists in the perception of direction, while the skin furnishes touch receptors, and there are nerves in joints and spindles in muscles which furnish the muscle sense referred to at pp. 423, 491, 517, and 616.

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* 'The Analytical Mechanism of the Internal Ear,' Sir Thomas Wrightson, 1918.

The bony semicircular canals have within them a membranous counterpart; between the bony and membranous structures is a fluid known as *peri-lymph*, while within the membranous is a second fluid known as *endo-lymph*. The vestibule has within it two membranous sacs, *utricle* and *saccule*, external to which is peri-lymph, while the sacs contain endo-lymph. Within each of these sacs is an elevation known as the *macula acustica*, the seat of the termination of the vestibular nerve. The nerve here terminates in cells known as hair cells, on the free extremities of which are cilia. The cilia of a bundle of such cells form stiff hair-like processes, and in connection with these there are fine solid particles of carbonate of lime known as **otoliths**. In the ampullæ of the semicircular canals are bodies similar to the maculæ acusticæ in which the fibres of the vestibular nerve terminate, but there are no otoliths. The peculiar nerve terminations briefly described above are bathed in the endo-lymph. Every movement of the head affects the fluid contents of that semicircular canal which corresponds to the plane in which the movement occurs, with the result that the fluid is displaced and causes a deflection of the stiff hair-like nerve-endings; the movement of these results in an impulse which is communicated to the cerebellum. The function of the utricle and saccule appears to be chiefly concerned with slow movements, equilibrium, and the position of the head, especially during the time the body is at rest. In these sacs the otoliths, affected by gravity, mechanically stimulate the nerve-endings.

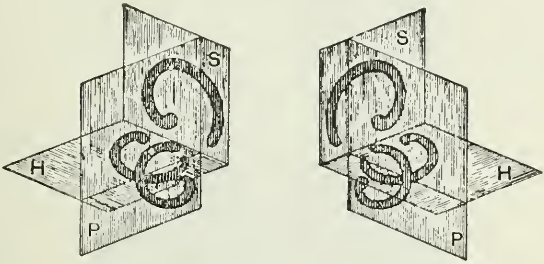

Fig. 194.—The Semicircular Canals (Diagrammatic) (Ewald).

H, Horizontal canal; S, superior vertical canal; P, posterior vertical canal. The two horizontal canals are in the same plane. The plane of the superior vertical canal of one side is parallel to the plane of the posterior vertical canal of the opposite side.

The function of the labyrinth, to quote the words of Sherrington, is to keep the world right side up for the organism by keeping the organism right side up to the external world. The labyrinth also exercises effects on the voluntary muscles (p. 436), there being a constant outflow of impulses from it which maintain the muscles in a condition of tonus, for it can be shown experimentally that unilateral destruction of the semicircular canals causes loss of muscular tone on the same side of the body; in cases of death it causes delay in the appearance of *rigor mortis*. The semicircular canals are also connected with the control of the ocular muscles and the maintenance of a horizontal pupil (p. 572).

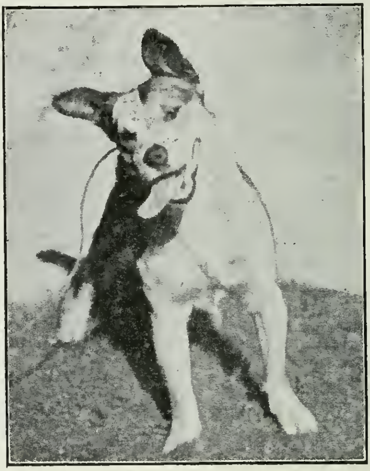

FIG. 195.—DOG TWENTY-TWO MONTHS AFTER DESTRUCTION OF RIGHT LABYRINTH (WILSON AND PIKE).

Unilateral destruction of the canals in cats produces a to-and-fro rolling of the eyes, muscular inco-ordination, and rotation of the head. It does not destroy the 'falling reflex' (see p. 488), though the body generally rotates in a direction away from the lesion. Destruction of the canals in the pigeon produces, among other symptoms, muscular inco-ordination and an inability to fly.

Unilateral destruction of the labyrinth does not produce in mammals the same degree of muscular inco-ordination as in birds. At first they readily fall towards the injured side and move with difficulty, always in the direction of the side of the lesion, yet the most pronounced symptoms are shown in the head and eyes. The former is turned towards the injured side (Fig. 195), and the eyeballs roll, the direction depending on the canal destroyed.

CHAPTER XVI

LOCOMOTOR SYSTEM

SECTION I.

Muscles, Joints, Tendons, Ligaments.

Muscles and Joints.—The structure of muscle, its innervation, and the phenomenon of a muscular contraction, have been studied. It is here intended to examine the muscles at work, and to ascertain what they are capable of effecting, and how they effect it. Speaking broadly, the skeleton is clothed with muscle; there are exceptions to this, such as the face and the limbs below the knee and hock, where the framework is uncovered, but generally the bones are clothed, the muscular covering of the limbs becoming progressively lighter from above downwards. The scapula and humerus, the pelvis and femur, are buried beneath a mass of muscle; over the radius and tibia the muscular structure is much less in bulk, and at the knee and hock it suddenly ends. The movements of the limbs of quadrupeds are of a simple character. Considered only in solipeds, these consist of a to-and-fro pendulum motion, and a limited movement in an outwards and inwards direction. This is infinitely more simple than in those animals furnished with a paw or hand. The limbs have to be flexed and extended, abducted and adducted, and both in the fore and hind legs these movements are carried out entirely by the muscles clothing or attached to the scapula and humerus, pelvis, femur, and tibia.* Speaking broadly, no muscles originate below the elbow or stifle joints.

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* A definition of the following terms employed in limb and joint movements may be desirable:

Flexion and Extension refers to either joints or limbs. To flex a limb is to bend it; to extend a limb is to straighten it. Nevertheless, this does not cover the entire ground; the foot, for instance, during the movement of flexion causes the pastern to become extended—viz., straightened. Conversely, when the foot is extended, the pastern is bent or flexed.

Abduction and Adduction.—These terms apply to limbs only. A limb is abducted when it is carried away from the middle line of the body. Similarly, it is adducted when drawn towards the middle line. The amount

This being so, it is evident that movements of the upper part of the limbs are automatically followed by movements of the lower parts.

Flexion and Extension.—It is usual to picture muscles at work from the appearance they present on the dissecting-room table; valuable as this is, it does not tell the whole story. It is only when muscles function that the fundamental principle is grasped that they are really never idle, and that even when not engaged in performing the more active duties for which they exist, they are still part of the animal machine, and engaged in the work of muscle co-operation. Flexion, extension, abduction, and adduction, are not the exclusive functions of individual muscles. A muscle is not, for instance, exclusively engaged as a flexor or extensor; it may be actively employed in flexion, or passively employed in extension; it may be actively engaged in extending one joint, and actively engaged flexing another; it may be actively flexing one joint, and automatically flexing its neighbour; it may be passively employed in extending one joint, and when active act as a flexor of another. Examples of these points will now be given, for if the machine at work is to be correctly visualised, the facts above stated must first be clearly grasped by the mind.

1. *A muscle may be a flexor when contracting, and an extensor when not active.* A good example of this is the flexors of the fore-limbs, which, when not contracting, are maintaining the elbow-joint firmly extended. Another is the *biceps brachii* (*flexor brachii*), which, when actively contracting, flexes the elbow-joint, and when passive is assisting, by means of a strip of tendon to the *extensor carpi radialis* (*extensor metacarpi magnus*), in keeping the knee firmly extended.

2. *A muscle may be engaged actively at one and the same moment in extension and flexion.* This is seen in the *superficial digital flexor* (*flexor perforatus*) of the hind-limb, which in extending the hock-joint flexes the pastern.

3. *A muscle may be actively engaged flexing one joint and*

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of abduction and adduction of the limbs is very small; it reaches its maximum in a 'cow-kicker' on the one hand, and on the other in a horse that 'brushes' from defective conformation, but especially in a 'weaver.'

Rotation is a term limited to joints, and the only joints in the limbs of the horse which can rotate are the shoulders and hip. Rotation of the stifle is produced in the hock and carried out in the hip-joint.

It is obvious that in all movements of flexion, extension, abduction, adduction, and rotation, the action is not an isolated one; the movements must work at least in pairs, and sometimes the entire series is employed. Take, for example, a horse 'cow-kicking': the limb must first be flexed, then forcibly extended, and at the same time abducted. To admit of this there must be rotation of the hip, and to allow the limb to recover its position adduction must follow.

automatically flexing its neighbour. The muscles which flex the stifle-joint automatically flex the hip.

4. *A muscle may in flexing one joint flex several others.* This is the case in the flexors of the fore-limbs, which flex knee, fetlock, pastern, and foot, at one and the same contraction.

5. *A muscle may be passively engaged extending one joint and actively employed in flexing another.* An example of this is the *tibialis anterior,* which with *peroneus tertius* (*flexor metatarsi*) is passively engaged by means of the cord which runs through their substance in maintaining the stifle extended, and when that joint is flexed is actively engaged in flexing the hock.

6. *Two parallel muscles, with a common tendon of origin, may act in opposite senses.* This is seen in the *tibialis anterior, peroneus tertius,* and the *anterior long digital extensor* (*flexor metatarsi* and *extensor pedis*); the one extends the foot, the other flexes the hock.

7. *A muscle may both passively and actively be an extensor only.* An example of this is the gastrocnemius muscle, which, whether the foot be on or off the ground, is an extensor of the hock.

It is possible for a muscle to be so anatomically situated as to appear to act as an extensor of one joint and a flexor of another, yet when the muscle is acting in the living animal it may be found to act only as a flexor, and never as an extensor. Sherrington has shown that this is the case with the *semitendinosus* muscle of the cat, which is so situated as to act as a flexor of the knee (stifle) and an extensor of the hip-joint; but experimentally it can be shown that the muscle always flexes the knee, and never extends the hip, for the reason that the hip flexor contracts at the same moment, and neutralises its action on that joint.

It has already been pointed out (pp. 435, 436, and 491) that even when the muscles of the body are apparently not acting they are in a condition of slight contraction, which is necessary for the maintenance of the standing attitude, and that it is only during the time the animal's weight is actually off its legs that the muscles can be considered to be at rest.

When a muscle contracts its antagonist is relaxed, and the nervous channel through which this is effected has been described under the head of ' reciprocal innervation ' (see p. 489). Where muscles act on a single joint, one as a flexor and the other as an extensor, the reciprocal nervous mechanism is easily understood, as the two muscles are direct antagonists. But when muscles are not exclusively devoted to one joint—in fact, affect two or more—the nervous mechanism is not so simple, for the reason that flexion at one joint may lead to extension at another. An example of this has already been given; the *semitendinosus* muscle is permitted to act only as a flexor of the knee (stifle) of the cat, and not as an extensor of the hip, and to secure this the latter joint is fixed by a contraction of its flexor muscles. In such cases the nervous mechanism is *identical*, not reciprocal, for the flexors of the hip contract in order to prevent extension of this joint, at the same moment as the semitendinosus contracts and flexes the stifle.

The condition revealed by this experiment is that flexor and extensor muscles, true antagonists, may contract together, co-operate, in order to fix a joint, so that another joint may be more effectively acted upon. Similarly, two extensor muscles may be actively employed some distance from each other in fixing the joint of a limb; they are not true antagonists; they are both extensors, and they act at the same moment; they are spoken of as 'partial antagonists.' The best example of this is afforded by the gastrocnemius muscle, which always acts as an extensor, whether during standing or in active movements, yet its origin from the femur is such that it might flex the stifle. It never flexes the stifle, for the reason that the muscles of the patella keep the stifle extended at the time the gastrocnemius is acting by keeping the hock extended. The patella muscles and gastrocnemius muscles are partial antagonists; they contract together and relax together, and by so doing insure that one joint is kept fixed in order that a muscle crossing it may act better on another joint. The innervation such muscles receive is identical.

When muscles have a muscular origin and a tendinous insertion, the direction in which their contraction occurs is from muscle to tendon; but when muscles are fleshy throughout, such as the long muscles found in the dorsal region, they may act from either end—for instance, in the group referred to they act from the neck end in kicking, and the croup end in rearing (Figs. 227, 228).

Tendons and Ligaments.—The chief function of ligaments is to hold bones in position. The greater the necessity for joint freedom, the fewer and simpler the ligaments. The shoulder-joint, for instance, has no special lateral ligaments. The range of motion is too considerable for these, so that tendinous insertion of the muscles takes their place. There is very much less motion in the hip, and the ligaments are centrally placed. In the other joints they are laterally situated, but from knee and hock to the foot a ligament seems to have been put in wherever space not otherwise occupied existed. Ligaments are also employed for holding floating bones like the patella and sesamoid in position. They knit together the various segments of the spine, and one of peculiar structure supports the head and neck. Ligaments may also run to tendons to enable the muscle to be partly cut off during the standing attitude. Two to the flexors of the lower limb of the horse undoubtedly assist the animal to sleep in the standing position while the muscles rest. They are known as **check ligaments.** Another kind of ligament peculiar to quadrupeds is a **tendo-ligament**—*i.e.*, a muscle with a tendon running completely through its substance from origin to insertion, which, when the muscle is not actively contracting, acts as a ligament, and when it is contracting plays its normal part of tendon. We shall see that this mechanism is employed both in the fore and hind legs for the purpose of maintaining a standing attitude with as little muscular strain as possible. A muscle may furnish a ligament to another muscle in order to afford it support. This is shown in the ligament detached by the *biceps brachii* (*flexor brachii*) to the *extensor carpi radialis* (*extensor metacarpi magnus*). A variation of this is a muscle detaching a ligament to a bone which is considerably out of its path—for instance, the ligament detached by the large *biceps femoris* (*triceps abductor femoris*) to the calcis.*

The elasticity of tendons and ligaments is considered later (p. 653). This subject has proved a fruitful source of difference of opinion, and the matter is by no means agreed upon yet.

The elasticity of muscle has been dealt with at p. 434, and to form a conception of what occurs to tendons under the influence of strain, the elastic property of muscle must not be forgotten. Nothing could well be more unlike in appearance, texture, and general physical characters, than muscle and tendon. Yet the soft, pulpy, friable material does not tear in the living animal, while the tendon attached to it may be torn apart. The only locomotor muscle in the horse's body which shows a disposition to rupture is the *flexor metatarsi*, and such a lesion is so rare that many have never seen it.

Colin tested the breaking-strain of muscles removed from a horse which had just been destroyed. The great extensor of the metacarpus broke at a tension of 988 kilogrammes (2,173 pounds); the flexor perforans of the fore-limb at 685 kilogrammes (1,057 pounds); and the flexor of the arm at 973 kilogrammes (2,140 pounds). In the hind-limb the extensor pedis muscle broke at 415 kilogrammes (913 pounds), the flexor of the metatarsus at 924 kilogrammes (2,032 pounds), and the flexor perforans at 510 kilogrammes (1,122 pounds). The extensors of the metatarsus ruptured at 616 kilogrammes (1,355 pounds), 687 kilogrammes (1,511 pounds), and 983 kilogrammes (2,162 pounds) respectively, but the muscles are not mentioned by name. It will be observed that the breaking-strain of the extensors is much higher than that of the flexors, that of the extensor of the metacarpus being nearly one ton. In the hind-limb there is a marked difference between the breaking-strain of the extensor pedis and flexor metatarsi muscles, though the two have a common tendon of origin. Finally, the relatively low breaking-strain of the flexor muscles is very evident. If the chief flexor of the fore-limb—a muscle which perhaps does half the work of propelling the body in the gallop—breaks at a tension of 1,507 pounds, we may be sure from this that the breaking-strain of its tendon is correspondingly low. As a matter of fact, muscular rupture during life is rare, and it may be urged that such post-mortem observations do not represent what occurs in the living condition. That is certainly true; nevertheless, it is suggestive that the low breaking-strain of the flexor muscles corresponds to the frequency with which during life the flexor tendons are sprained.

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* Anatomists are responsible for the confusion existing in muscle nomenclature. Where possible, the writer has followed Sisson in modern terminology, inserting the known equivalent in brackets. There are six names for the biceps femoris muscle!

Levers.—The muscles are attached to bones, and the latter form various angles with each other, which are opened and closed during progression. The mechanical aid introduced in order to effect this is the lever. Levers are of three orders, depending upon the relative positions of the power, fulcrum, and weight. A *lever of the first order* is mainly a lever of extension, the power being at one end, the weight at the other, the fulcrum between. A good example is the extension of the head on the neck; the weight is the head, the power lies in the neck, the fulcrum is the joint between the head and neck. A *lever of the second order* is not common in the body. The weight lies in the middle, the fulcrum and power at either end. When the fore-foot is on the ground supporting weight, the foot is the fulcrum, the body through the elbow-joint is the weight, the power lies in the biceps muscle acting on the ulna. A *lever of the third order* is the lever of speed and flexion. In it the power lies between the fulcrum and weight. In the flexing of the arm the biceps is the power, the fulcrum lies above it in the elbow-joint, the weight lies below—viz., the weight of the limb. This is a lever which sacrifices power for speed; it is therefore wasteful, but necessary in the limbs.

Function of Muscles.—The muscles of the skeleton have a twofold function to perform—they move the body and they maintain its attitude (p. 435). Accordingly, so long as the animal is not actually lying down, the muscles are in constant action, though the effort required to maintain attitude is less exhausting than that necessary to moving and carrying weight. **A standing attitude** is maintained by the flexible limbs being rendered rigid, and this is effected by the muscles keeping the joints locked. For this purpose they receive a constant stream of impulses, and if these are withdrawn for ever so brief a period, the body falls under its own gravity.

It requires a greater muscular effort to maintain a standing attitude in the fore than in the hind legs, owing to the fact that the fore-limbs are not attached to the body by any joint, and are solely dependent on masses of muscle for support. When a horse sleeps in the standing attitude, his muscles not infrequently lose their tonic impulses, and he falls, but always front first, never hind first, and never in a heap. Long before his knees have reached the ground the muscles have secured control once more, and he seldom falls farther than his fetlocks.

It seems quite legitimate to regard the muscular union between the thorax and the fore-limb as a joint. There are no bones resting on each other, no synovia; but where the scapula has its largest range of movement there is a remarkable amount of areolar tissue, which renders movement easy. The whole central area beneath the scapula and humerus not occupied by muscular attachment is filled with this easily-moving, apparently gaseously distended, crepitant, areolar tissue, over which the fore-legs glide on the chest wall as freely as if the parts were a large, well-lubricated joint. The animal's body is slung between the fore-legs, and the muscle principally, if not wholly, engaged in this important function in the thoracic portion of the *serratus magnus*. The tendinous cover of this immense muscular plate imparts additional strength, and is present in all muscles where strain is constant or long continued (see p. 424). The serratus magnus, on contracting, also draws the posterior and upper part of the scapula downwards; this is antagonised by its cervical portion. This muscle is a good example of a single muscle being so arranged in its fibres that they may act together or in opposition. During the standing attitude the fibres of this muscle are acting together, but in opposite directions, in order to maintain the scapula in a fixed position. During locomotion the portions are acting alternately (see Fig. 199).

The fixation of the scapula is the first essential step towards a standing attitude, and it is secured by the *serratus magnus, rhomboideus*, and *trapezius* (see Figs. 198, 199). The humerus below has now a firm bed to press against, as the scapulæ are

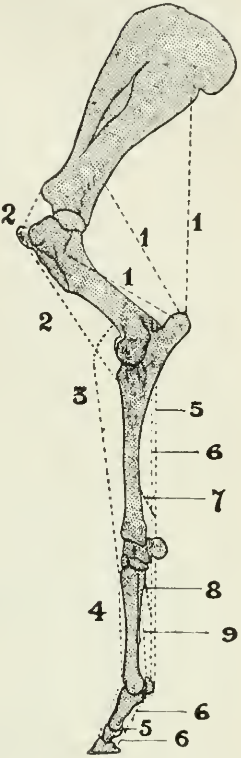


FIG. 196. — BONES OF THE FORE-LEG OF THE HORSE IN THE ATTITUDE OF STANDING.

The dotted lines show the principal mechanism by which the limb is kept rigid.

1, 1, 1, The great triceps muscle; 2, the flexor of the arm; before insertion it gives off a slip of tendon to the extensor of the metacarpus, 3; 4, the extensor tendon of the foot; 5 and 6, the flexors of the foot; 7 and 8, the check ligaments; 9, the suspensory ligament.

prevented from being driven through the withers by the serratus. It is essential for the humerus that the shoulder-joint should be fixed and the elbow-joint locked. The large muscular mass of the triceps, acting from the humerus and scapula on the ulna, is mainly engaged in effecting this (Fig. 196, 1). The more powerfully the triceps contracts, the more firmly is the beak of the ulna forced into the olecranon fossa of the humerus. It is this mechanism which keeps the elbow-joint locked. But what has previously been said about the absence of exclusiveness in muscles being borne in mind, it is evident that the flexors of the fore-leg act passively on the elbow and keep it firmly extended (Fig. 196, 5 and 6), while the *biceps brachii* (*flexor brachii*), through its connection with the main extensor muscle of the limb, helps to keep the scapula in position and the shoulder-joint from opening in front (Fig. 196, 3). This is a good example of co-operative antagonism. Here we see the flexor of the arm, extensor of the leg, and extensor of the elbow, all of which are antagonists when actively contracting, working together to one common end. The tendon running throughout the length of the biceps is of invaluable assistance in keeping the shoulder-joint fixed while the limb is in the standing position; it acts, in fact, as a ligament from scapula to radius (Fig. 196, 2).

The shoulder and elbow being fixed, the next joint, the knee, is far more easily controlled. From the knee to the foot it is only necessary to prevent the joints opening in front in order to maintain the limb rigid and upright (p. 435), and to insure this each segment of the limb is furnished with an extensor tendon (Fig. 196, 3 and 4). There is a large one to the knee, and another to the pastern and foot, each of which is in turn reinforced for extra strength. The muscles which manipulate this locking apparatus run from the humerus, cross the front of the elbow-joint, and are distributed segment by segment until the foot is reached. Their efficacy in locking the fore-limb from the elbow to the foot depends upon the elbow-joint itself being firmly extended and locked. The large knee extensor receives powerful assistance from the *biceps brachii* in the form of a ligament which runs from the biceps to the extensor (Fig. 196, where 2 and 3 meet).

The position thus created is as follows: The biceps during the standing attitude, though not out of action, is not engaged in flexing the elbow. It is a flexor muscle which, we have just seen, is passively resisting the triceps, but it does not hesitate to help an extensor, an opponent, during the time it is not otherwise actively employed on its own special duty. This is a good example of the non-party feeling shown by muscles, and their desire for general rather than special utility.

The weight from the elbow to the foot is carried on the flexor muscles of the arm, of which there are five, three not proceeding below the knee, to the back of which they obtain attachment, and two which run the entire length from elbow to phalanges

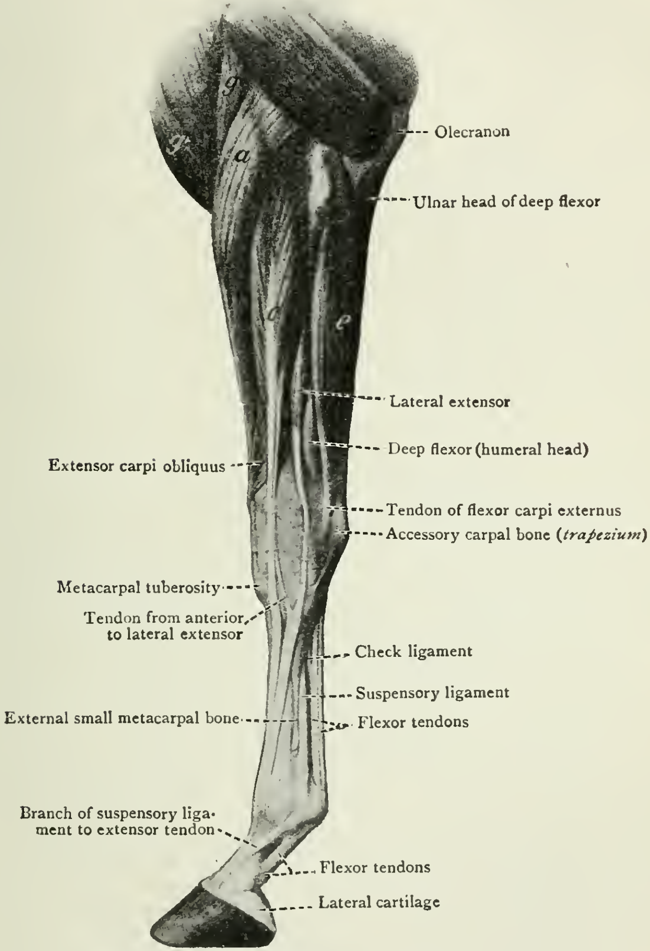

g
g′
a
c
e
Olecranon
Ulnar head of deep flexor
Lateral extensor
Deep flexor (humeral head)
Extensor carpi obliquus
Tendon of flexor carpi externus
Accessory carpal bone (*trapezium*)
Metacarpal tuberosity
Tendon from anterior to lateral extensor
Check ligament
Suspensory ligament
External small metacarpal bone
Flexor tendons
Branch of suspensory ligament to extensor tendon
Flexor tendons
Lateral cartilage

FIG. 197.—MUSCLES OF OUTSIDE OF NEAR FORE-LIMB OF THE HORSE (ELLENBERGER-BAUM-SISSON).

a, Extensor carpi radialis ; g, brachialis ; g′, anterior superficial pectoral ; c, anterior or common digital extensor (extensor pedis); e, flexor carpi externus.

All these flexor muscles are characterised by the presence in their substance of a considerable amount of fibrous tissue, and both at the knee and elbow are fused with the fascia of the fore-arm, by which means additional support under continuous strain is obtained. But it is by the two long flexors, the *superficial* and *deep digital* (*flexor perforatus* and *perforans*) (Figs. 196, 5, 6; and 197), that the main support to the bony column is given, and this is obtained through the limb bending forward at the fetlock and these two tendons passing beneath and supporting the bent joint. The weight of the body presses the fetlock to the ground. The counteracting force of the flexor tendons sustains that weight, and maintains the fetlock in position. They are not the only mechanism supporting the fetlock, for there is the suspensory ligament, of which later; but the flexors are the chief support, and, if they are divided, the fetlock sinks appreciably closer to the ground. The changes occurring in the fetlock-joint when an animal from injury or other cause is compelled for some time to support its body weight entirely on one limb serves to explain the mechanism of the joint. It is rarely that the muscular portion of the supporting flexors gives way under the strain, but commonly the tendinous portion, and this is well seen at the fetlock-joint. The bursa of the tendons at the part is dry; the tendons themselves are dry, yellow, and shrunken. The interior of the fetlock-joint reveals nutritive changes, brought about by long-continued compression. The articular cartilage has become so thin that the bone has the barest possible covering, the joint is dry and yellow, and so intense has been the pressure that the actual pattern of one joint surface may be imprinted deeply on the adjacent bone, and this imprint is made on the posterior part of the articulation, and not on the anterior; in other words, the pressure falls behind.

The two long flexors running from elbow to foot are assisted in their duties as weight-bearers by means of so-called **check ligaments** (Figs. 196, 7, 8; 197). These ligaments are running, not from bone to bone, but from bone to tendon, and make a tendon function as a ligament by cutting off, as it were, the muscular attachment above. The perforatus above the knee and the perforans below it both receive a check ligament, which under the long-continued strain of support enables the flexor muscles to slightly relax and obtain a much-needed rest.

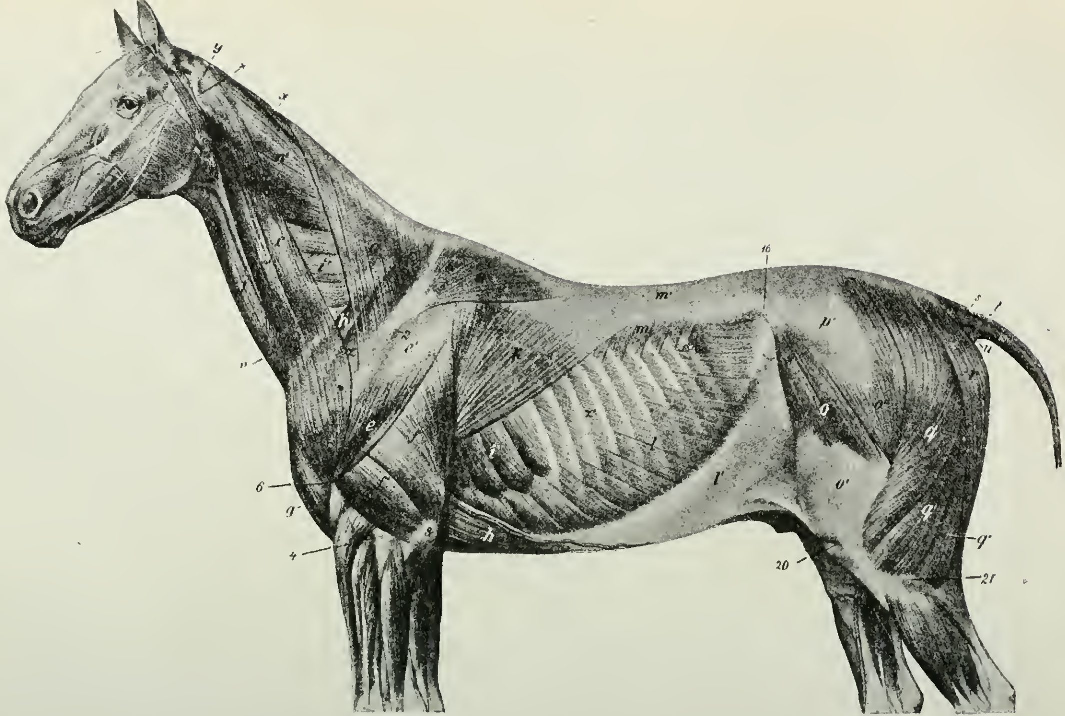
The mechanisms below the fetlock are a continuation of those above it, the same extensor and flexor tendons being employed from elbow-joint to foot. The slope of the pastern is maintained by the flexors of the leg, and though a joint exists between the second and third phalangeal bone, its function, when the limb is in the standing attitude, is not in evidence. In looking at the slope of the pastern, the eye always regards it as one bone, instead of two. The reason is obvious. There is very little movement in the joint between the corona and suffraginis at any time, and there is still less in standing. They are united by a dense network of ligamentous material, and, as we shall see later in studying the limb in movement, the chief motion occurring in the pastern bones is between the corona and pedis.

The fore-limb is kept vertical and the pastern bent by the insertion of the perforans tendon into the pedal bone; every joint from the elbow to the foot is locked by its extensor tendons and supported by its flexors, the fascia of the arm binding up and supporting both groups.

In the hind-limbs the standing attitude is simpler, owing to the existence of the **hip-joints** beneath the horizontal spine. The attitude assumed by the legs is the result of flexion in some joints, extension in others. The hip-joint is flexed by the *psoas magnus, iliacus, tensor fasciæ latæ, gluteus superficialis* (*gluteus externus*), and *pectineus* muscles. Considering the enormous amount of muscular tissue belonging to the hind-quarters, it is rather remarkable that so little of it is required for hip-flexion, for the above, relatively speaking, are not bulky muscles. The extensors of the hip-joint, on the other hand, are very large—*i.e*, the insertions of the large *biceps femoris, gluteus medius*, and *semimembranosus* (see Figs. 198, 199, and 200).

The above groups of muscles fix the head of the femur rigidly so far as to-and-fro and outward movements are concerned, but the joint has also to be supplied with support on its inner side, and this is effected by the *great* and *small adductors* and *gracilis*. The resultant of the pull of these muscles on the hip-joint is the position assumed by the femur in standing, and the angle it forms with the pelvis depends upon whether the limb is bearing weight or resting. The joint below the hip is the *stifle*, and the part this plays in attitude is considerable, for no flexion of the hind-leg can possibly take place without the concurrence of the stifle. The stifle is flexed by means of the *biceps femoris, semitendinosus*, and *gracilis* (Figs. 198, 200); it is extended by the *rectus femoris* and *vasti* muscles (Fig. 199). Unless these latter concur, flexion of the stifle is impossible. So slight, indeed, is the effort required to keep the stifle rigidly extended that if *one* hand grasps the muscles inserted into the patella, and presses the bone back on the femur—the horse having just been destroyed—no ordinary force employed at the foot-end of the limb can flex the hock, and the hock cannot flex without the stifle flexing.

Tendo-Ligaments of the Thigh.—From the above it is evident that very little muscular effort is required to keep the largest joint in the body fixed during the standing attitude. The stifle is kept extended not only by the muscles inserted into the patella, but also by the contraction of the *anterior digital extensor* (*extensor pedis*), *peroneus tertius*, and *tibialis anticus* (*flexor metatarsi*, muscular and tendinous division)—a pair of muscles (Fig. 201)



[FIG. 198.—SUPERFICIAL MUSCLES OF THE HORSE (ELLENBERGER-BAUM-SISSON).

The panniculus, excepting the cervical part, has been removed. *a*, *Cervical trapezius* ; *a'*, *thoracic trapezius* ; *c*, *c'*, *mastoido-humeralis* (*levator-humeri*); *d*, *sterno-cephalicus* ; *e*, *deltoid* ; *f*, long head of *triceps* ; *f'*, external head of *triceps* ; *g*, anterior superficial *pectoral* ; *h*, posterior deep *pectoral* ; *h'*, anterior deep *pectoral* ; *i*, *thoracic serratus* ; *i'*, *cervical serratus* (*serratus magnus*); *k*, *latissimus dorsi* ; *l*, *oblique abdominis externus* ; *l'*, aponeurosis of *l* ; *m*, *serratus posticus* ; *m'*, lumbo-dorsal fascia; *o*, *tensor fasciæ latæ* ; *o'*, *fascia lata* ; *o''*, superficial *gluteus* ; *q*, *q'*, *q''*, *biceps femoris* ; *r*, *semitendinosus* ; s, *t*, *u*, muscles of tail; *v*, *cervical panniculus* ; *w*, *splenius* ; *x*, *rhomboideus* ; *y*, tendon of *trachelo mastoideus* and *mastoido-humeralis* ; *z*, *supra-spinatus* ; x, wing of atlas; 2, spine of scapula; 4', external epicondyle of humerus; 6, deltoid tuberosity; 8, olecranon; 16, external angle of ilium; 20, patella; 21', external condyle of tibia.

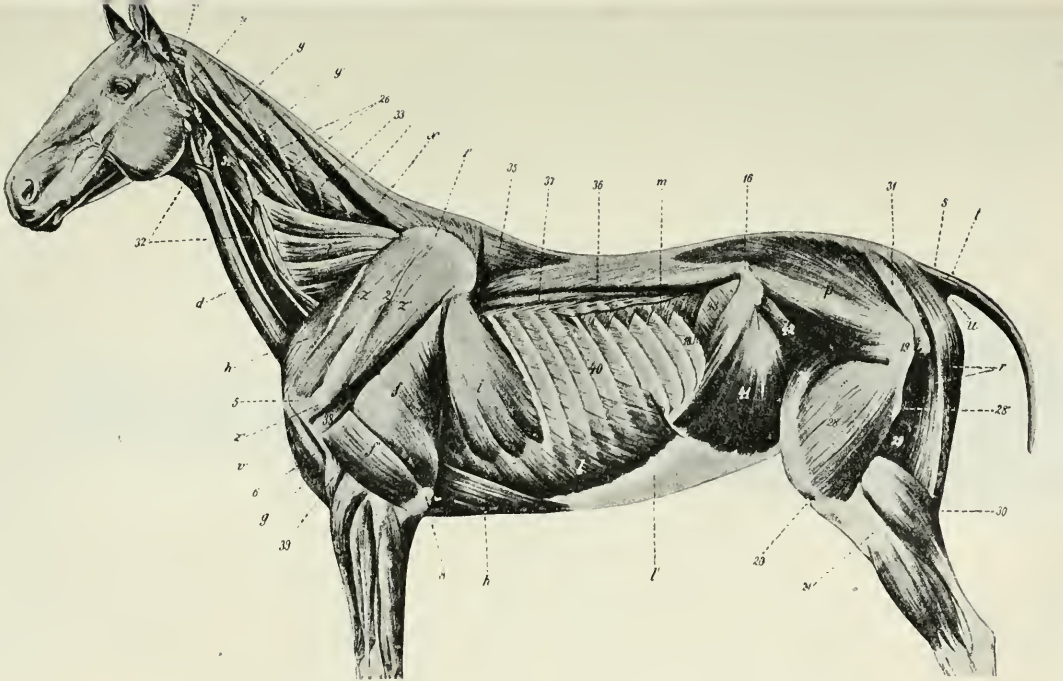


Fig. 199.—Deep Muscles of the Horse (Ellenberger-Baum-Sisson).

Long head of *triceps* ; *f′*, external head of *triceps* ; g, anterior superficial *pectoral* ; *h*, posterior deep *pectoral* ; *h′*, anterior deep *pectoral* ; *i*, *thoracic serratus* ; *i′*, *cervical serratus* ; *l*, *oblique abdominis externus*, and *l′*, its aponeurosis, the posterior part of which has been removed; *m*, *serratus posticus* ; *p*, *gluteus medius* ; *r*, *semitendinosus* ; *s*, *t*, muscles of tail; *v′*, *biceps brachii* ; *x*, *rhomboideus* ; *y*, *y′*, *trachelo-mastoideus* ; *z*, *supra-spinatus* ; *2′*, *infra-spinatus* ; 1, cartilage of scapula; 2, spine of scapula; 5, external tuberosity of humerus; 6, deltoid tuberosity; 8, olecranon; 16, external angle of ilium; 19, trochanter major; 20, patella; 21′, external condyle of tibia; 26, articular processes of cervical vertebræ; 28, *vastus internus* ; 28′, *rectus femoris* ; 28″, trochanter tertius; 29, *semimembranosus* ; 30, *gastrocnemius* ; 31, sacro-sciatic ligament; 33, *complexus* ; 34, *rectus capitis anterior major* ; 35, *spinalis dorsi* ; 36, *longissimus dorsi* ; 37, *transversalis costarum* ; 38, *teres minor* ; 39, *brachialis* ; 40, external *intercostal* ; 41, *oblique abdominis internus* ; 42, *iliacus* ; 43, *transversalis abdominis*.

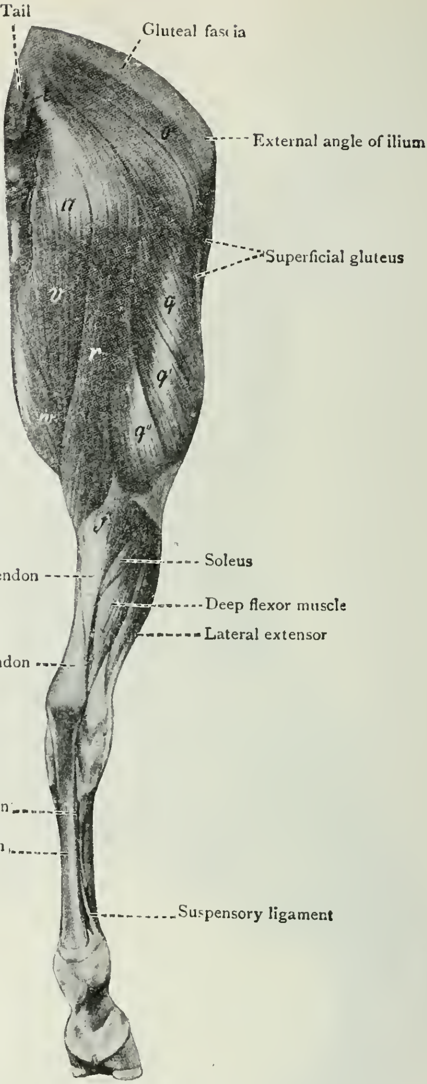

Tail
Gluteal fascia
External angle of ilium
Superficial gluteus
Soleus
Gastrocnemius tendon
Deep flexor muscle
Lateral extensor
Superficial flexor tendon
Deep flexor tendon
Superficial flexor tendon
Suspensory ligament
o″
17
v
q
r
q′
w
q″
f

FIG. 200.—MUSCLES OF OFF HIND-LIMB OF HORSE (ELLENBERGER-BAUM-SISSON).

17, Position of *tuber ischii* ; *o*″, superficial *gluteus* ; *q*, *q*′, *q*″, *biceps femoris* ; *r*, *semitendinosus* ; *v*, *semimembranosus* ; *w*, *gracilis* ; *f*, *gastrocnemius.*

attached to the external condyle of the femur by means of a common tendon. The tendon runs from the stifle to the hock-joint, and is a cord of great strength, acting not only as a tendon to the muscles which envelop it, but also as a long straight ligament (Fig. 202, 3). Chauveau describes the action of this tendo-ligament as possessing the property of flexing the hock automatically in conformity with flexion of the stifle, but he also regards its other use as that of keeping the stifle-joint extended. It is impossible for the flexor metatarsi to act while the stifle is kept locked, and there can be no doubt that the action of the cord as a long ligament is of great value in relieving

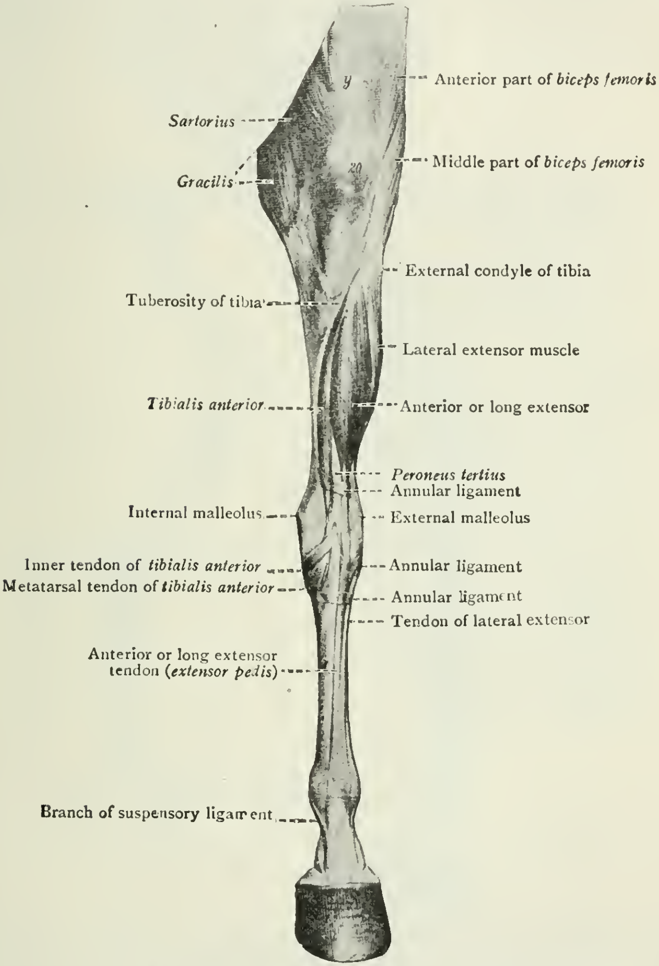

y
Anterior part of *biceps femoris*
Sartorius
20
Middle part of *biceps femoris*
Gracilis
External condyle of tibia
Tuberosity of tibia
Lateral extensor muscle
Tibialis anterior
Anterior or long extensor
Peroneus tertius
Annular ligament
Internal malleolus
External malleolus
Inner tendon of *tibialis anterior*
Annular ligament
Metatarsal tendon of *tibialis anterior*
Annular ligament
Tendon of lateral extensor
Anterior or long extensor tendon (*extensor pedis*)
Branch of suspensory ligament

FIG. 201.—MUSCLES OF NEAR HIND-LIMB OF HORSE, ANTERIOR VIEW (ELLENBERGER-BAUM-SISSON).
y, *Rectus femoris* ; 20, patella.

the strain from the flexor metatarsi muscle. That the cord is not absolutely essential to standing may be determined experimentally by dividing it, or clinically by the rupture which occasionally occurs. It is the antagonist of a similar tendo-ligament at the back of the tibia, which runs from the femur to the calcis, the function of which is to oppose hock-flexion (see Fig. 202, 2).

The dotted lines indicate the powerful mechanisms for maintaining the limb in a rigid condition. 1, 1, The muscles which keep the patella drawn up and the stifle-joint locked; 2, the *gastrocnemius* and *flexor perforatus* muscles, both keeping the hock extended in opposition to 3; 3, the flexor of the hock and metatarsus automatically affected by 1. In 2 and 3 tendinous cords run from end to end, and so act as ligaments, keeping the parts in the relation prescribed by the patella without great muscular effort. 4, The perforatus below the hock; 5, the perforans; 6, the check ligament; 7, the suspensory ligament; 8, the extensor of the foot; 9, the *gluteus medius* (*maximus*) keeping the hip-joint extended.

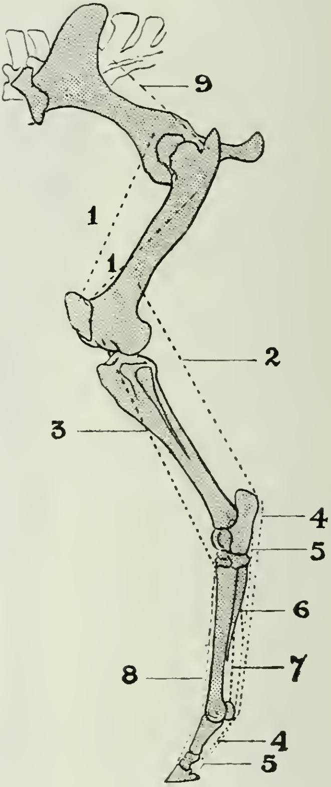


FIG. 202.—BONES OF THE HIND-LEG OF THE HORSE IN THE ATTITUDE OF STANDING.

The Hock.—The muscles which keep the hock extended (Figs. 202, 2; 203) are—(1) The *gastrocnemius*, running from the femur to the calcis, to which it is attached. It is an active extensor when the foot is off the ground, a passive extensor when the weight is resting on the limb. (2) The *superficial digital flexor* (*flexor perforatus*), which runs from the femur to the calcis, to which it is attached, forming a tendinous cup into which the point of the calcis fits, and subsequently running down the back of the limb to be inserted into the second phalanx. This muscle is almost entirely tendinous. It is the tendo-ligament (Fig. 202, 2) antagonistic to the flexor metatarsi (Fig. 202, 3) previously described. During the attitude of standing it relieves the constant strain which would otherwise be imposed on the gastrocnemius, and maintains the hock extended. It is not only an extensor of the hock, but one of the flexors of the lower limb.

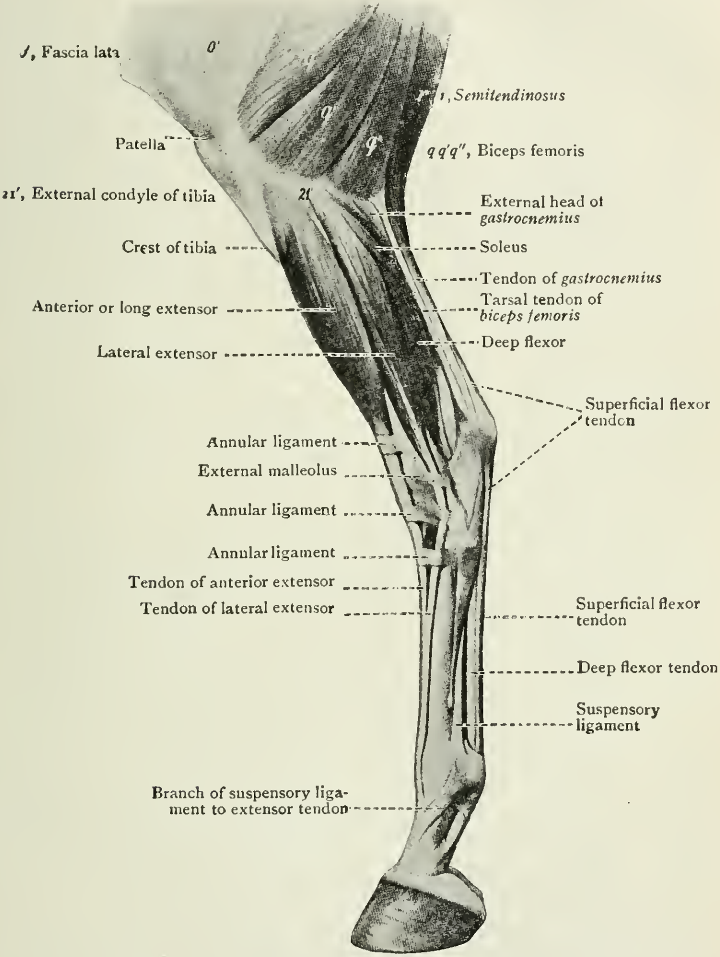

J, Fascia lata
O'
r 1, *Semitendinosus*
O
Patella
q'
q q'q'', Biceps femoris
21', External condyle of tibia
21'
External head of *gastrocnemius*
Crest of tibia
Soleus
Tendon of *gastrocnemius*
Anterior or long extensor
Tarsal tendon of *biceps femoris*
Deep flexor
Lateral extensor
Superficial flexor tendon
Annular ligament
External malleolus
Annular ligament
Annular ligament
Tendon of anterior extensor
Tendon of lateral extensor
Superficial flexor tendon
Deep flexor tendon
Suspensory ligament
Branch of suspensory ligament to extensor tendon

FIG. 203.—MUSCLES OF LOWER PART OF THIGH, LEG, AND FOOT OF HORSE, EXTERNAL VIEW (ELLENBERGER-BAUM-SISSON).

The Reciprocating Action of Stifle and Hock.—From what has been said, it is evident that flexion and extension of stifle and hock are identical in action. When the stifle is extended, the hock is automatically extended, nor can it under any circumstances flex without the previous flexion of the stifle. There is no parallel to this in the body. The two joints, though far apart, act as one, and they are locked by the drawing up of the patella, and in no other way (Fig. 202, 1). The so-called *dislocation of the stifle* in the horse is a misnomer. That the patella is capable of being dislocated is beyond doubt, but the ordinary condition described under that term, when the stifle and hock are rigid while the foot is turned back with its wall on the ground, is nothing more than spasm of the muscles which keep the patella drawn up (Fig. 202, 1, 1). The moment they relax the previously immovable limb and useless foot have their function restored as if by magic, but are immediately thrown out of gear in the course of a few minutes as a recurrence of the tetanus of the patellar muscles takes place. The fascia of the thigh, like that of the arm, is a most potent factor in giving assistance to the constant strain imposed on the muscles of the limbs during standing.

Below the hock the hind-limb is arranged like the fore, the deep flexor (*perforans*) receiving additional support from the 'check ligament,' as in the fore-leg (Fig. 202, 6).

The natural **attitude of standing** adopted by the horse is to rest on three legs—one hind and both fore. If he is alert, he stands on all four limbs; but if standing in the ordinary manner, he always rests one hind-leg. He does not remain long in this position without changing to the other. Hour by hour he stands, shifting his weight at intervals from one to the other hind-leg, and resting its fellow by flexing the hock and standing on the toe. He never spares his fore-limbs in this manner in a state of health, but always stands squarely on them. The moment he places one fore-foot in advance of its fellow—'pointing,' as it is termed—the experienced eye knows that something is wrong. Many years ago the writer suggested that the periodical resting of the hind-feet was the possible explanation of their freedom from navicular disease. The horse rests the fore-feet only when they are already subjects of this disorder.

Distribution of the Weight on the Limbs.—The fact that the animal rests the hind-limbs, and never the fore, suggests that the weight carried by the former is greater than that carried by the latter. The reverse, however, is the case. The fore-legs carry from 9 to 19 per cent. more weight than the hind. The weight on the fore-limbs is increased when the head is depressed, and reduced when it is raised. The latter movement displaces the centre of gravity backwards, and throws more weight on the hind-limbs, for the head of the horse is very heavy, being from 40 to 50 pounds in weight, more or less, depending on size and breed.

The Centre of Gravity.—During the standing attitude this lies near to the intersection of a horizontal line below the shoulder-joint by a vertical line passing about 6 inches behind the elbow. During locomotion, jumping, draught, etc., the position is constantly shifting from front to rear and from side to side, depending on the position of the body and the pace.

Lying Down.—The attitudes assumed by a horse in lying down are quite characteristic. He has only two positions—one flat on his side, with the legs and head fully extended, and the other with the head and spine raised, sitting obliquely on his chest. He cannot sit directly on the sternum, owing to its sharp edge, so the body inclines to one side in order to avoid it. In this attitude of repose both knees and hocks are bent, all four feet are brought under the body and arranged on a plan, which is never departed from. If, for instance, he is sitting on his chest inclined to the near side, the near fore-foot is placed close to the breast-bone, the elbow touching the ground—in fact, the body is resting largely on the near elbow. The near hind-foot is under the abdomen, the outer part of this limb, both hock and shank, resting on the ground. The off fore-foot lies close to the elbow, but outside it. The elbow does not rest on the heel of this foot, as is so frequently taught, and consequently never suffers injury from the heel of the shoe. The off hind-foot is flexed and brought forward towards the elbow, while the point of the hock of this limb rests on the ground. A 'capped elbow' never occurs from the heel of the shoe, but is due to the underneath elbow coming in contact with the ground. Similarly, a 'capped hock' may be aggravated or originate from resting on the point of the hock when lying. The horse, as a rule, sleeps fully extended on his side, but, should he sleep in the chest position, he rests the chin on the ground, often everting the lower lip, so that the teeth take the pressure. Cattle and sheep repose on the chest. The flat sternum is perfectly adapted to this, the only position normally adopted. During sleep they turn the head round to one side, the nose being placed towards the flank.

The **Act of Rising** is always performed in one way by horses and cattle, and in either animal the methods are reversed. No horse can rise until he has placed his fore-legs out in front. The first effort made is to unbend either knee alternately, and get the feet out in front, resting on the heels. The hind-legs are well flexed, the feet placed under the centre of the belly, and the animal reaches the standing position by means of the hind-legs, with the aid of the fore. The body follows the head, and if the head be kept down no horse can rise. All ruminants rise tail foremost. Resting on both knees, they raise the hind-quarters, straighten the limbs, and then rise in front.

Joints.—Before examining the second function of muscles—viz., the production of locomotion—it is necessary to consider again the question of joints. These have been studied in connection with their static function; they must now be looked at from their kinetic aspect.

Whenever two bones come together a joint is formed and an arrangement provided against the production of friction. Whenever any two surfaces meet, one of which is moving on the other—such as tendons passing through grooves or working over bony projections—similar anti-friction appliances exist. We have even ventured to regard the adjustment of the fore-leg on the chest wall as a joint, although wholly muscular, and have pointed out (p. 637) in what way friction is provided against. It has been shown that the joints of the limbs of the horse are furnished with automatic appliances for maintaining position with the least muscular effort, and enabling the animal to stand continuously for long periods. The features now to be considered are those connected with the movements of joints.

The **Shoulder-Joint** is remarkable for the small surface afforded by the scapula, and the large area existing on the humerus. This allows great freedom of movement in both a to-and-fro and a side-to-side direction. There is no bone in the body the movements of which resemble those of the scapula, and there is no joint which resembles that formed by it with the humerus. There are no separate ligaments to the joint; the tendinous insertions of the muscles are the ligaments, and this arrangement would appear to be associated with the immense freedom required in the rolling action of one bone on the other. Both in the fore and hind limbs the two upper bones of the leg are arranged to form an obtuse angle with each other, and this is peculiar to quadrupeds. In the biped the humerus is not bent from the vertical, nor are the femur and tibia. The object of the bending is to insure great rapidity of action and to destroy concussion; there is far less jar in dropping on a limb in which the column of bones is bent towards each other than in a column which is vertical. The scapula and humerus form an angle of about 120 degrees. The shoulder-joint is lifted—viz., the fore-limb is advanced—by only one muscle, the *mastoido-humeralis* (*levator humeri*) (Fig. 198). Arising from a region as high as the head and atlas, this immense muscle is alone responsible for advancing the limb. The numerous and complex movements occurring throughout the whole length of the leg on the shoulder being raised may here be outlined. The shoulder cannot be advanced with the foot on the ground, so the weight must first be transferred to its fellow; the elbow-joint is next unlocked by a relaxation of the extensor muscles, which are inserted into the ulna; the *biceps brachii* (*flexor brachii*) next contracts to carry the arm forward, and by so doing assists to flex the elbow,* the flexor muscles of the back of the limb contract in order to flex the foot and all the joints as high as the knee. The column of bones being broken as described and the whole limb made flexible, it is carried forward, the thoracic portion of the *serratus magnus* and *trapezius* pulling one angle of the scapula backwards, and the *latissimus dorsi* flexing the humerus on the scapula. The limb having been advanced sufficiently, the flexible column of bones is once more

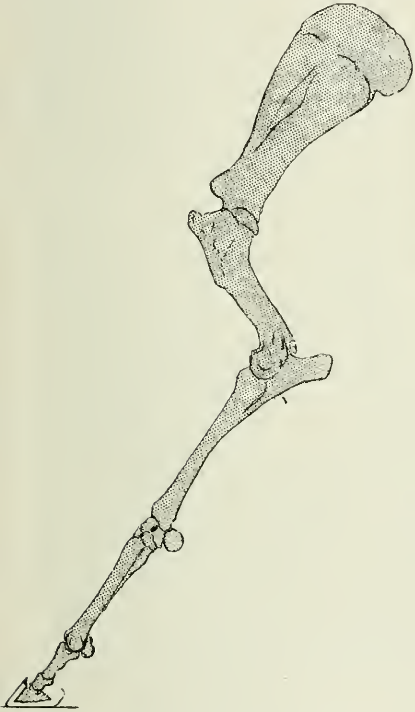


Fig. 204.—The Position of the Column of Bones of the Fore-Leg when the Foot makes Contact with the Ground.

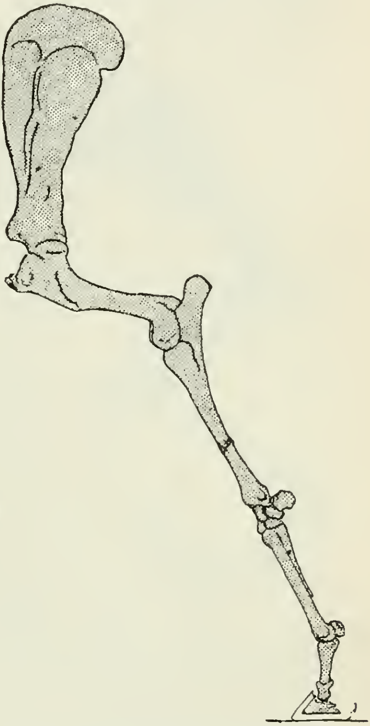


Fig. 205.—The Position of the Column of Bones of the Fore-Leg preparatory to Final Propulsion.

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* At this moment it is lifting a weight of about 17½ pounds (8 kilos) in a riding-horse, this being the weight of the limb from elbow to foot, exclusive of the shoe.

made rigid. First the extensors of the carpus and foot act, straighten the limb at the knee, and put the foot in position to receive the weight of the body when it comes to the ground. The effort to advance the leg is trifling, and the foot having made contact, the limb being in the position shown (Fig. 204), the real work now begins, for the body has to pass over the limb, while the leg remains fixed and rigid from elbow to foot. The muscles which pull it over are the *latissimus dorsi* acting on the humerus, and the large *deep pectoral* muscle (see Fig. 199), which, running forward from the ninth or tenth ribs and sternum beneath the fore-leg to the shoulder-joint, pulls the whole shoulder-joint backwards, and causes the body to rotate over the limb. It is powerfully assisted in this by the *cervical serratus* and *trapezius* drawing the scapula forwards and upwards, and by the large head of the *triceps* pulling on the ulna. At the end of the movement the column of bones is in the position shown in Fig. 205, and the final act of the limb is about to occur—viz., its propulsive motion. To effect propulsion, the limb remains rigid, while the long flexors of the arm straighten the pastern until little more than the toe of the foot is on the ground; then, with a sudden sharp contraction of these muscles, the body is propelled upwards and forwards, the limb being flexed (Fig. 206), carried to the front, unbent, and again placed on the ground.

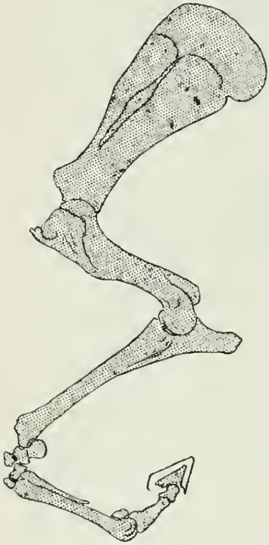

FIG. 206.—THE COLUMN OF BONES FORMING THE FORE-LEG BROKEN UP, THE LIMB SHORTENED BY FLEXION AT SHOULDER, ELBOW, KNEE, FETLOCK, AND BEING CARRIED FORWARDS.

The **Elbow-Joint** has already occupied attention, more particularly in connection with its locking during the attitude of standing. During locomotion extensive hinge-like motion occurs, which is abnormally exaggerated in high-steppers. The hinge has two condyles and a ridge on the humerus, which fit into a reverse moulding on the radius. The internal condyle is much the larger, and occupies about half the entire articular surface. These condyles, during flexion of the joint, turn the knees outwards. If they throw them out too far, the leg below the knee is thrown in, and so causes ‘brushing’ and ‘speedy cutting.’ This movement is best seen from above when mounted. Though a hinge-joint, the arm appears to describe a semicircle in the sweep it makes on flexion of the elbow. It is greatly exaggerated in some horses.

The **Knee-Joint** consists of three main joints and numerous minor ones. The articulatory surface of the radius with the upper row of knee-bones has no parallel in the body; it is a surface both deeply concave and markedly convexo-concave. The concavity and convexity on the radius form condyles of which the inner is more curved than the outer. The concavity on the anterior part of the radio-carpal articulation rests on the convex surface of the upper row of knee-bones, and in this way a firmer and closer union between these surfaces is obtained, such as is needed in the upright condition of the limb. But when this joint is flexed, the convex posterior surface of the radius comes forward; this depresses the *scaphoid* (*radio-carpal*), and produces between it and the *semilunar* (*intermediate carpal*) a very important movement by which the foot is thrown slightly outwards, probably with the object of enabling it to clear the opposite limb. The upper joint of the knee possesses the largest range of motion, the middle joint very much less, the lower joint hardly doing more than gliding on its fellow. Percivall pointed out many years ago that the *trapezoid* rests wholly on the head of the inner splint bone, which explains the frequency with which this bone becomes affected with ‘ splint.’

The **Fetlock-Joint** forms a special variety of articulation, one which is firm and rigid anteriorly, elastic and yielding posteriorly. This is effected by introducing two sesamoid bones into the fetlock articulation, and suspending them between ligaments; the structure by means of which the sesamoids are suspended is the **Suspensory Ligament** (Fig. 197). This runs from the back of the large metacarpal bone to the fetlock, receiving insertion into the sesamoids. The latter are floating bones, and, speaking more generally, perhaps, than an anatomist would permit, they are embedded in ligamentous material which keeps them in their place. The supsensory ligament supports them above and laterally; the sesamoidal ligaments keep them fixed below. The anterior face of these bones forms the posterior face of the fetlock-joint.

There is no other joint in the body the mechanism of which has received so much attention as that of the fetlock and suspensory ligament. The rival theorists have been divided on the question of the elasticity of the suspensory ligament. Gamgee (senior) regarded it as absolutely non-elastic; he did not believe that it supported the sesamoids, but regarded it as acting powerfully in flexing the foot (p. 669), being brought into action or set free according to the position of the limb. It was he who destroyed the notion once and for all that the sesamoids moved up and down.

The fetlock-joint furnishes the only example in the body of a bone placed vertically resting on one placed obliquely. The metacarpal rests on an inclined plane in the form of the suffraginis, and but for the sesamoids would slip off at the back. It is one of the functions of the sesamoids and suspensory ligament to keep this bone in its place, and so support the fetlock under stress.

The sesamoid bones are also intended to furnish the fetlock-joint with a yielding articulation, which receives the weight of the body when the foot comes in contact with the ground. At the moment this occurs the whole pastern from fetlock to foot becomes more oblique, giving the appearance of sinking, which in reality occurs. The sinking, however, is not due to displacement of the sesamoids, but to increased obliquity of the pastern under stress, owing to which the suspensory ligament is under great strain. It does not appear to be reasonable to deny it some degree of elasticity—viz., the power to stretch slightly and then return to its original length (p. 662); but the stretching is not great, and can be reproduced on a limited scale by lifting up the opposite fore-leg, and observing the tense, sharp lines produced in the suspensory at the moment the fetlock descends, through increased obliquity of the pastern. The evidence that the suspensory supports the fetlock is seen in the effect of dividing it, which brings the fetlock appreciably nearer to the ground, while the evidence that the suspensory ligament possesses only limited elasticity is furnished clinically by the frequency with which it is sprained. If it were highly elastic, a sprain would be a difficult matter. No one, for instance, ever heard of the only elastic ligament in the body being sprained—*i.e.*, the *ligamentum nuchæ*—but a ligament of this nature in any part of the limbs would be useless. If tendons and ligaments were highly elastic, the efficient action of muscles would be destroyed, for during contraction their tendons would be stretching instead of pulling.

It is quite easy to show that in the ordinary standing attitude the sesamoid bones, together with the posterior half of the metacarpal articulation, bear the weight of the body, while the anterior surface of the suffraginis and metacarpal takes but a small share. The two movements of the fetlock-joint are flexion and extension. Flexion in every other joint in the body but the fetlock begins by bending, but when the fetlock is to be flexed the pastern has first to become straight before it can be bent backwards. Flexion of this joint is accomplished by the *perforans* and *perforatus*, while extension is brought about by the *extensor* of the foot and *suffraginis*. The more the foot is extended, the greater the strain on the sesamoids, and the slip of the suspensory ligament which joins the extensor tendon (Fig. 197) may at this time be associated in drawing the sesamoids closer to their articulating surface, as the fetlock becomes more extended. Or the slip may be considered in the light of an extension of the suspensory ligament, in order to afford it increased surface of attachment. The use of the slip, however, is not very evident, and we have never seen it sprained, which is the best evidence that its share is not very important.

The suspensory ligament becomes sprained when the flexor muscles tire, for the fetlock-joint is supported not only by the suspensory ligament, but by both flexor tendons. Division of the *perforatus* tendon or of the *suspensory ligament* produces very little effect on the dropping of the joint; division of the *perforans* creates evident effect, but it requires division of both flexors to bring the heel of the foot to the ground (see Fig. 207, 3).

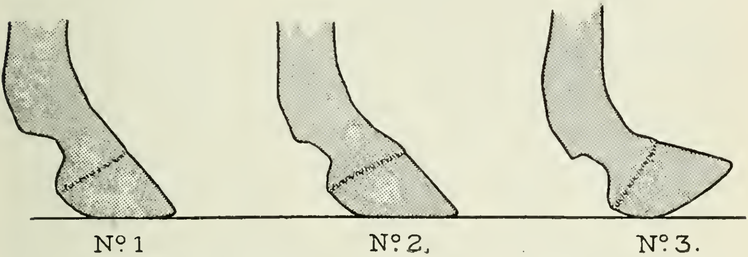

Fig. 207.—Effect of Experimental Division of the Suspensory Ligament and Flexor Tendons on the Obliquity of the Pastern (after Lishman).

1. Division of the *suspensory ligament* has caused the fetlock to drop a little.
2. Division of the *flexor perforatus* tendon has caused slight sinking of the fetlock.
3. Division of both *flexors*, *perforatus* and *perforans* tendons, brings the heel of the foot to the ground, and causes the toe to turn up.

The fetlock-joint does not come to the ground unless all the structures are divided.

Pastern-Joint.—This joint, formed between the first and second phalangeal bones, allows of limited flexion and extremely limited extension. It is, in fact, specially arranged to act during extension, as if the first and second phalanx were only one bone, and no joint existed between them. This function comes into play when the body rotates over the foot on the ground—*i.e.*, during the period the body is passing from the position in Fig. 204 to that in Fig. 205. When the limb passes the vertical, the two bones, owing to the arrangement of their ligamentous connections, move as one on the pedal articulation; in other words, the corona and suffraginis are immovably locked, and for the time being the joint between the fetlock and foot is obliterated. As the locking is entirely ligamentous, the strain must be considerable. When the foot comes to the ground, concussion to the pastern joint is saved by the fibrous plate which exists at its posterior part. This plate is on the corona, and is hollowed out for the reception of the rounded surface of the suffraginis.

The **Pedal-Joint** is formed by three bones—the second and third phalangeal and the navicular bone. The chief movements occurring are flexion and extension. This joint is the centre of the entire movement of the leg; the body rotates over it. Relatively it is a small articulatory surface built up and strengthened by the hoof, the cartilages of the foot, the flexor and extensor tendons of the foot, and the connecting ligaments peculiar to the bones forming the joint. It is a yielding or elastic joint, on account of the introduction of the navicular bone into its posterior part; this functions as a sesamoid, and by yielding under pressure counteracts shock. The pedal-joint is so deeply buried within the foot, and strengthened by the various structures named, that though it is the centre of movement during the passage of the body over the limb, it is practically immune from the diseases of locomotion, so common in other joints. Not so the joint last considered—the pastern; it is frequently the seat of trouble, probably due to the strain on the ligaments when the bones become locked during extension.

Joint-Locking.—Repeated attention has been drawn to joint-locking, and the example last given of the mechanism enables a more comprehensive statement to be made. The whole of the joints in the fore-leg of the horse from knee to coronet are locked during extension. The only joints where movement is occurring are the shoulder, elbow, and the articulation between the corona and pedis. The locking occurs when the limb on the ground is no longer vertical—when, in fact, it is assuming the position shown by the fore-leg in Fig. 205; from that moment every degree of further extension locks knee, fetlock, and pastern the tighter. This renders the limb from the arm to the foot as rigid as if it were composed of one piece of bone. It also explains why the posterior part of the knee-joint is one mass of interlacing ligamentous structure.

The **Hip-Joint** has a wide range of movement in flexion, extension, and rotation; but owing to the position of the *round ligament* (*ligamentum teres*), outward movement at right angles to the body is limited. The pubio-femoral ligament, which is confined to the horse, is derived from the prepubic tendon of the abdominal muscles. It is far from clear why a slip of tendon from the abdominal muscles should require to be inserted into the articulating head of the femur. During inward rotation of the thigh—as, for example, when the foot is on the ground and the body is passing over it—the pubio-femoral ligament is rendered tense (Sisson). When the ligament is long, the stifle turns outwards, the points of the hock turn in, and the condition known as ‘ cow-hocks ’ is produced. It will be observed that the production of cow-hocks has nothing to do with any part but the hip-joint. The insertion of the round ligament into the inner side of the head of the femur limits the outward movement of the limb, and is generally considered to explain why a horse so seldom ‘ cow-kicks.’

The Stifle-Joint.—This is the largest joint in the body, and is built on quite different lines to any other. A large convex surface on the femur is placed resting on a flat surface on the tibia, with absolutely no bony cavity in which to rest or play. Shallow cavities are furnished by two plates of cartilage, which receive the condyles of the femur, and on which they rest quite superficially. It will be observed that, with this exception, no preparation exists on the tibia for the formation of this immense joint. Nothing could be more unlike in appearance than the in-contact ends of femur and tibia. The discs of cartilage, which take the place of bony cups, no doubt allow of considerable flexion and freedom of movement, but in a joint the arrangement is unreliable, and consequently the two bones are held together by two crucial ligaments running in opposite directions. These ligaments are somewhat twisted on each other, and when the joint is flexed the posterior ligament is rendered taut. Extension and flexion are the two principal movements of the stifle; during each of these the discs of cartilage on the tibia slide forward or backward on the bone in conformity with the movement of the femur, the movement of the external condyle and its cartilaginous cup being greater than that of the internal. The above is not the only joint formed by the stifle. In front is the patella, playing over two large convex surfaces, the trochleæ of the femur. The patella is, like the sesamoids, a floating bone; it appears to move up and down, but as it is attached below, this is impossible. It is the trochleæ of the femur which move, the large inner one doing most of the work. The muscles inserted into the patella and the muscles which flex the hip-joint are direct antagonists. It is impossible for the hip, or even so remote a joint as the hock, to flex so long as the patella muscles are maintained in a condition of contraction. When they relax, flexion of the hip-joint is permitted by means of the muscles already considered (p. 641), the tibia is drawn up by the *biceps femoris* and *semitendinosus* (Figs. 198, 200), the trochleæ of the femur appear above the patella, the *flexor metatarsi* is placed in operation and flexes the hock, and as the stifle becomes more and more flexed, the bulk of the whole joint increases, and is turned outwards from the abdomen, in order to accommodate its increase in size. This turning outwards of the stifle, a feature seen in any pace, but particularly well marked in the trotting horse, is not due to any mechanism in the stifle, but to the hock-joint. It will be shown presently that the ridges on the astragalus, through their action on the tibia, turn the stifle outwards.

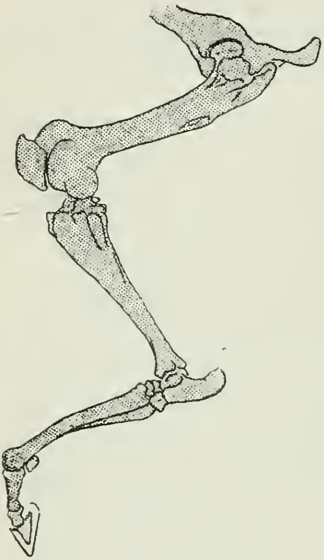

FIG. 208.—FLEXION OF THE HIND-LIMB.

The **Hock-Joint** is not only of physiological, but of the greatest clinical interest, owing to its being the frequent seat of lameness. It is a hinge-joint, and a hinge in such a position on the limb must be of great strength to resist the tendency to close under the influence of the body weight. In fact, the hock-joint, unlike the knee, to which it corresponds, is under the constant stress of extension, which is the reason why, in spite of the automatic appliances with which it is furnished for keeping it open, the joint is always being alternately closed for the purpose of rest. The long lever at the back of the joint, in the form of the calcis, is a lever of the first order; it is the lever of power, and the strain on these muscles will be realised when it is remembered that the whole weight of the hind-quarters is supported by the *gastrocnemius* and *flexor perforatus* through their insertion into the calcis. The strain is largely removed by the introduction of a tendo-ligament—viz., a cord running from end to end within the muscle, and forming its two attachments, by which means it is capable of relieving much of the strain from the muscle. The existence of two such cords in the hock is described at p. 645 (see Fig. 202, 2, 3).

The two movements of the hock are flexion and extension; the extension, which occurs during the attitude of rest, is dealt with at p. 646. The extension of locomotion is carried on by the same mechanism—viz., the gastrocnemius muscle, and the tarsal tendon running from the biceps femoris muscle (*biceps* *abductor femoris*, or *long vastus*) to the calcis (see Fig. 203). It is seldom that the eye can witness *extreme* extension of the limb—*i.e.*, when the tibia and metatarsus form their nearest approach to a straight line (Fig. 209); the movement is altogether too quick during the gallop. Its nearest representation is obtained when a horse ‘stretches’; the limb is then thrust out behind, rigid and taut, and the hock fully extended. From the position of backward extension the limb is brought forward by flexion of the tibia on the femur, and the femur on the pelvis, by mechanisms already discussed, when flexion of the hock-joint follows (Fig. 208). The limb now comes forward under the body, and the foot, which was previously flexed, is extended, in order to come to the ground heel first or flat, depending on the pace. The leg is then in the position of forward extension (Fig. 210). While the extensor of the foot is producing this action with the assistance of the lateral extensor, the *flexor metatarsi* (*Tibialis anterior*) has to relax in order to unbend the hock. The flexor of the hock and the extensor of the foot have a common tendon of origin (Fig. 202), so that a remarkable physiological peculiarity now occurs, in that a pair of muscles having a common tendon of origin are enabled to function in a diametrically opposite manner, the extensor of the foot contracting, the flexor of the hock relaxing. The flexor of the metatarsus, besides the common tendon at the femur, has a muscular addition from the tibia (Fig. 201), and it would be quite competent for this muscular portion to relax or contract independently of its neighbour. The difficulty lies in explaining the behaviour of the common tendon to a pair of

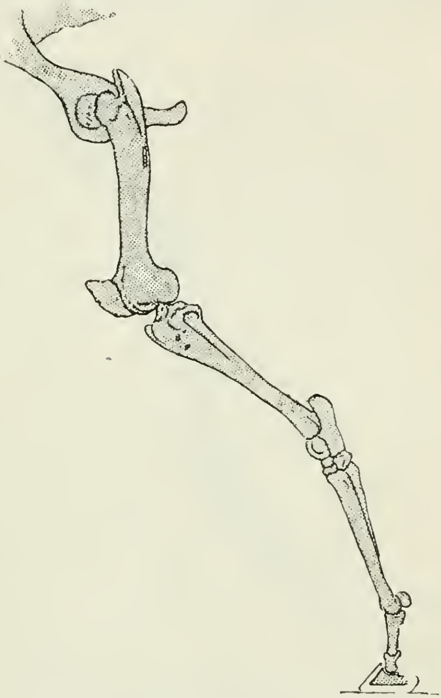

Fig. 209.—Extension Backwards of the Hind-Limb.

muscles running parallel to each other and functioning in an opposite sense.

Chauveau, many years ago, described the tendon of the flexor metatarsi as a conducting cord (Fig. 202, 3), the function of which was to regulate the flexion of the hock by purely automatic action. He conceived that this automatic effect was brought about by stifle flexion. There can be no doubt that the position of the cord is greatly altered by flexion of this joint. The more the stifle is flexed, the higher the cord is drawn in the direction of the hip; and as it is fixed below to the metatarsus, the latter has to follow automatically (Fig. 208). But we cannot concur in thinking that the conducting cord can effect flexion without muscular aid, and believe that the *flexor metatarsi* must take an active share, in spite of the difficulty of explaining precisely how this is effected without inducing antagonistic action in its neighbour, with which, as we have seen, it possesses a tendon in common.

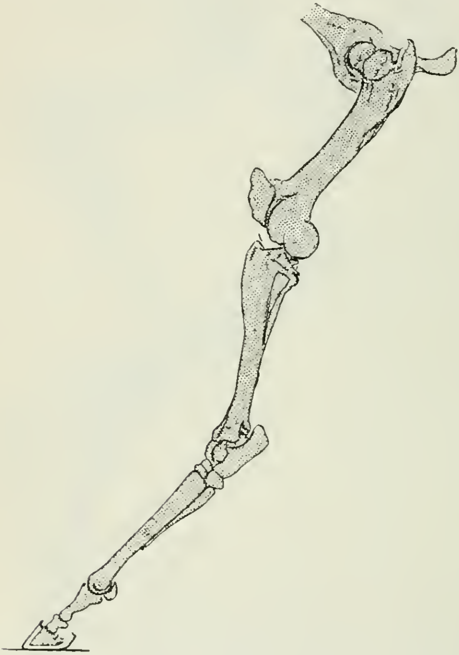

FIG. 210.—EXTENSION FORWARDS OF THE HIND-LIMB.

The next point to engage attention is the astragalus, the hinge-like ridges of which in the horse are arranged obliquely like the threads of a screw. No animal other than the horse has oblique ridges to the astragalus. It might appear at first sight that their effect on flexion would be to turn the leg out below the hock. But the horse does not carry his legs in this way. When the hock is flexed, the parts below it are carried forward true to the front; if the ridges on the astragalus acted on the lower limb, the legs would be flung outwards. The screw of the astragalus affects the joint above, and not the limb below it. It turns the stifle outwards, producing the stifle action so much admired in trotting horses. When the hock is flexed, the stifle is turned outwards; when it is straightened, the stifle is turned inwards, and in some horses the effect of the screw-turning movement is to cause the foot, when it comes to the ground, to be twisted, and the point of the hock to be thrown outwards. This gives the appearance of a wrench, but is natural to some horses. Animals with a considerable space between the last rib and the stifle-joint do not need to have their stifles turned outwards. In the horse the last rib and stifle are so close together that the latter has to be directed away from the abdominal wall.

The movement between the small bones in the hock-joint is very slight, and is not a to-and-fro sliding motion, such as might be expected, but partakes of the nature of a rotation or twist on each other. This fact will be understood when it is remembered that the centres of the small bones of the hock are attached to each other, and to the astragalus and metatarsus, by interosseous ligaments centrally placed, which practically prohibit any movement but that of slight oblique twisting. This fact is revealed also by the friction marks in diseased joints.

The range of motion between the tibia and astragalus is considerable, yet it is not fully exercised in all paces. It is only in jumping and the gallop that the astragalus moves from end to end on the tibia. In order to prevent excessive flexion, two stops or buffers exist on the tibia, which come into contact with two rests on the astragalus. The outer stop is the larger of the two, but owing to the obliquity of the face of the tibia, the inner one is the first to make contact. When the hock-joint is fully flexed, only the anterior part of the tibia is in contact with the astragalus; the posterior part is raised from the trochlea, and a space exists between them. The pressure through the hock falls mainly on its anterior part, and on the inner rather than the outer side. This is the region most frequently affected with disease. The tissues at the back of the hock suffer when the fore-hand is raised during jumping, and may also suffer strain when the hind-limbs receive the weight of the body in the gallop; but the chief trouble affecting the hock is one occurring to the bony structures.

The Functions of the Limbs in Relation to the Causes of Lameness.—The bones forming the flexible columns of the limbs, with their tendons, ligaments, and enveloping tissues, are exposed to strain. It is evident that the strain is greatest during movement, but it requires some little experience with horses to realise the stress to which the parts are subjected even when the animal is doing no work. For instance, laminitis is common when horses are standing in a fixed position, as on board a ship, though nothing more than the weight of the body is being supported. A horse injured in one leg may frequently give way in its fellow through the latter supporting extra weight, so that, quite apart from work, the legs may suffer in their effort to support the weight of the body. During work the strain on the limbs is of two kinds—viz., that which arises when the body is propelled from the ground, and that which occurs when the body comes to the ground. One may be spoken of as the strain of propulsion, the other as the strain of impact. Of the two, the strain of propulsion is the greater, and in consequence the fore-limbs which propel the body during the fast paces suffer from injury to a far greater extent than the hind-limbs which receive it. Strain and concussion in the limbs are provided against in several ways. The bony columns of the legs, it will be observed, are broken up, the smallest segments being nearest the ground, the largest away from it. The bones forming the column are frequently arranged at an angle, by which means direct jar is minimised. This is especially the case in the hind-limbs, which receive the weight of the body in all fast paces. Joints of a non-rigid kind are formed in three parts of the limb, all being close together and but a few inches from the ground. One exists within the foot, another at the fetlock, and an imperfect one at the pastern. These offer an elastic rather than a rigid resistance. The muscles, tendons, and ligaments also contribute to this elasticity. Muscles, we have seen, are perfectly elastic; it is a property which belongs to them; neither tendons nor ligaments are regarded as elastic, though more than once attention has been drawn to the fact that there must be some give and take in these tissues, some stretching and recovery. That neither is capable of severe extension is undoubted, and normally, so long as the muscles maintain their complete command of the limb, both tendons and ligaments are in the matter of withstanding strain subordinate to them. When muscles tire and lose their elasticity, their tendinous attachments suffer, and it is almost invariably at this time that sprains of tendons occur. When a horse tires, it is the fore-leg flexors which sprain, for the reason that the burden of propelling the body falls on the flexor muscles of the fore-limbs; the flexors of the hind-limbs only receive the weight when the body comes to the ground, and, relatively speaking, rarely suffer.

The extensor tendons of the limbs never suffer, for the work done by their muscles does not necessitate a powerful contraction such as occurs in the flexors when in the gallop they propel 9 hundredweight (460 kilogrammes) of material a distance of several feet through the air. This is why the flexor muscles tire in spite of their tendinous intersections, and the moment this occurs the tendons have to take the shock.* One can imagine that for some strides the check ligaments are useful accessories in helping the tendons to deal with fatigued elongated muscles, but the attempt to propel the body from the ground with tired muscles and a stretched tendon causes the latter to yield, and one or both tendons partly or completely give way either where the subcarpal check ligament joins, or between it and the fetlock. The muscles never rupture, and the tendons rarely yield at any other spot than between the fetlock and the middle of the shank. Both tendons in this region are at their smallest. Sprains of the flexor tendons do not occur at a walk, nor in the stable from slipping, nor on the road from trotting; they occur during the canter and the gallop, for the reason that it is in these two paces only that one fore-leg is called upon to propel the entire body weight.* The suspensory ligament sprains when insufficient support is given by the tendons of tired flexor muscles to the fetlocks and pastern. Other ligaments in the limbs may give way through an actual wrench—*i.e.*, the subcarpal ligament in draught-horses, caused by backing, or while endeavouring to prevent slipping on greasy roads; but here the ligament is caused to act in an unnatural manner, both fore-legs being out in front of the body. Sprains of the connecting ligaments of the pastern-joint—viz., that formed between the suffraginis and corona—and some consider of the hock, may be due to wrenches during work, and form the origin of future disease in these regions. Lateral motion in either of these joints is normally very limited, and wrenches while passing over broken ground must occasionally occur. Notwithstanding, the writer never remembers to have seen a case of lameness, other than arising from external injury, occurring to the pedal joint where the lateral ligaments are well marked. The essential point, however, is that sprains of the flexor tendons or suspensory ligament, due to wrenches, are practically non-existent.

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* We have seen (p. 635) that there is a great difference between the post-mortem breaking-strain of the flexor as compared with the extensor muscles of the fore-limb.

The causes generally discussed above are mainly acting as the limb leaves the ground; but there are others occurring during impact, producing what is conveniently termed 'concussion.' These jar the foot and the bones at the lower end of the column. Of this the clearest evidence is furnished by fractures of the pastern, which always occur as the foot comes to the ground. When the suffraginis, and rarely the corona, break, the line of fracture is in nearly every case very similar, showing either that a common cause is at work, or that these bones possess inherent lines of weakness.

We have glanced at two periods during locomotion when injury may occur; there is one other, and that is the time during which the body is rotating over the foot. It has been shown that the fore-leg below the elbow is intended to open and close in one direction only; for instance, the foot may be made to touch the back of the elbow, but it cannot be made to touch the front of the knee. When the body is rotating over the foot, a point is reached where the bones between the elbow and the foot are locked together and rotate as one piece (see p. 656). At this time there is a great strain on the locking arrangement, and considerable compression of the small bones which form the end of the limb. Between the suffraginis and corona the strain would appear to be greatest, on account of the small size and slender nature of the joint, and for the reason that it is placed next to the centre of rotation. Clinically it is recognised that this region is the seat of often incurable lameness. Whether this originates from a sprain of the ligamentous material which forms the 'locking' apparatus of the pastern, or from injury (concussion) to the bones themselves, is not clear; probably both processes are at work.

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* The flexor tendons give way in the American trotting horse, though not so frequently as in race-horses in this country. It occurs when the animal tires. It has been said above that horses do not sprain their tendons while trotting, but obviously this does not refer to racing. Further, the animal, when match-trotting, does not use his limbs in the same way as in the common trot. On this important point, see p. 671. The writer is indebted to Professor Pierre Fish, New York State Veterinary College, Cornell University, and to Drs. W. Sheppard, M.R.C.V.S., and Grenside, U.S.A., for information regarding lameness affecting the American trotter,

There are some seats of lameness where apparently specific causes are at work which should not baffle discovery. It is the upper and *never* the lower articulatory surface of the corona which is involved in ringbone, though these surfaces are only an inch or two apart; it is the under and *never* the upper surface of the navicular which is affected with caries, though these surfaces are not half an inch from each other. It is the inside and *not* the outside of the hock-joint which is affected in spavin. The seats of these affections are not matters of accident, but due to definite causes which the writer considers are intimately concerned with the physiology of the parts.

In concluding this brief outline of the physiological aspect of lameness, attention must be drawn to the fact that it is the small and not the large joints which usually suffer; it is not those at some distance above, but those nearest to the ground. It is not the fibrous tissues so frequently as the denser structures. Speaking generally, three-fourths of the cases of lameness occur in the fore-limb, and three-fourths of the seats of lameness in the fore-limb are found within a few inches of the ground. The detection of the seat of lameness will ever be one of the most difficult duties of the veterinary surgeon, and a thorough knowledge of the anatomy and physiology of the limbs is the first step towards forming a sound judgment.*

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* The advanced student may profitably consult the following papers by the writer: 'The Pathology of Navicular Disease,' *Veterinary Journal*, vol. xxii., 1886; 'Some Diseases of the Joints of the Horse,' *Journal of Comparative Pathology and Therapeutics*, vol. v., 1892; 'Sprains of Tendons and Ligaments,' *idem*, vol. vii., 1894.

SECTION 2.

Locomotion.

The movement of the limbs during locomotion is a question both of theoretical interest and practical importance. This is especially true in the case of the horse, owing to the fact that he is one of the few domesticated animals which have to work, and to the frequency with which this results in lameness. There are features connected with lameness which can be explained only when the method by which the limbs are employed during progression is understood. Limb movements in the biped are relatively very simple; in the quadruped there is both simplicity and complexity, the latter owing to the rapidity of movement and our inability to observe four legs at one and the same time. All paces but the simple trot defy accurate visual analysis. It was not until instantaneous photography came to the aid of physiology that the question of the sequence and method of limb combinations during locomotion was finally settled. The name of Muybridge and his co-workers will for ever remain identified with this inquiry. Without instantaneous photography it was impossible to analyse fast paces like the gallop, though it is distinctly remarkable how very close some of the older observers got to the truth. Exactitude, however, was not obtained, nor criticism silenced, until 1878, when the camera, under the direction of Muybridge, settled the question of animal locomotion for ever.

Step and Stride.—When a man walks, the *step* is the distance between the two feet measured from toe to toe or other convenient points in symmetry; two such steps constitute *a stride*, which is the distance covered by a foot from the time it leaves the ground until it again reaches it. For quadrupedal locomotion the same definition holds good, but the introduction of another pair of legs renders it rather more complex. In the quadruped the **step** is the distance between any two hind-limbs or any two fore-limbs, or any fore and hind limbs employed in moving together. The **stride** is the distance covered by a fore or hind limb from the time it leaves the ground until it again reaches it. The step and stride can be measured from the impressions left on the ground, though great care is required in order to discriminate carefully between the various feet. In the same horse a step from one hind-foot to its fellow is not always the same length as a step from one fore-foot to its fellow. In the faster paces like the gallop the step taken by the fore-legs is longer than that taken by the hind-legs. In the horse one stride at a walk contains two steps; in any faster pace than the walk the stride embraces a period in the air, during which there are no feet on the ground. In the trot, the legs being used in diagonal pairs, there are two steps and two springs to the stride; in the canter and gallop there are two steps and one spring.

Limb Velocities.—It must not be forgotten that in the slowest paces the legs in motion are moving faster than the horse. Take the case of the walk at five miles an hour: the moving legs have to overtake the body, and in order to do that within the brief period allowed they must move at least double as fast as the horse. In the gallop Muybridge showed that in a horse covering nineteen yards in a second (thirty-nine miles an hour nearly) the advancing limb was brought forward with an occasional velocity of forty yards a second, or nearly eighty-two miles an hour. It is not a matter for surprise that so much doubt and difficulty existed in regard to locomotion before the introduction of instantaneous photography.

The ordinary exposures given by Muybridge were the one-thousandth part of a second, though much shorter exposures than these were also employed. During the one-thousandth part of a second a horse galloping as above may move forward $\frac{7}{10}$ inch, and the moving foot $1\frac{1}{2}$ inches, so that shorter exposures had to be employed for high velocities.

Even when the order and method of moving the limb is known, it is very difficult, excepting in the slowest paces, to catch a glimpse of the real movement in any other pace than the trot. The limbs are as confusing as the spokes of a rotating wheel, while the body of the horse itself helps in no slight way to divert attention. To obviate this, the writer finds that the best method of seeing the limbs working is by looking at them through a narrow slit in a card, so held that only the legs are seen through the slit, the body being cut off.

The paces commonly employed by the horse are the walk, trot, canter, and gallop. There are others, such as the amble and the rack, neither of which is popular in this country, nor, indeed, is the latter employed for any other purpose than in one form of American racing. In all these paces the limbs are employed in different combinations. In the walk, for instance, a broad base of support is required, so that during a stride for half the time there are two legs and half the time three on the ground at one and the same moment. In the trot for half the time there are two legs on the ground and half the time the body is in the air. The arrangement is different in the canter, and again different in the gallop. Each pace has its own system of combinations, and when all the possible combinations are classified they amount to fourteen for the four legs. For instance, the number of different ways in which a single limb may be employed is obviously four, the possible combination with two legs is six, and the various combinations with four legs employed in progression is fourteen,

The Walk.

This pace is relatively slow; an ordinary horse walks about four miles an hour, and it would seem that, considering each limb can be distinctly observed, the movements would be easy to follow. As a matter of fact, to watch them is bewildering. The walk begins from a fore-leg. If a horse from rest begins to walk, one or the other fore-leg will be found the first to advance; there is no special choice shown as to whether it will be a near or an off leg, though an animal may time after time start with the same limb. This is not the generally accepted opinion outside the veterinary world. Muybridge himself says:

> 'When a horse is standing with the weight of the body equitably distributed over his fore-legs, and under these conditions commences to walk, the initiatory movement will invariably be made with a hind-foot.'

Borelli, who wrote on animal mechanism towards the end of the seventeenth century, described the walk as beginning with a hind-foot, but this has never been accepted by any veterinary writer. Percivall and Gamgee especially attacked it. Hayes says: 'As a rule a horse begins the walk with a fore-leg.' This suggests he has seen a hind-leg initiate the movement—in fact, he describes the sequence of limb movements which occur when a hind-leg is the first to start. It seems a remarkable fact that, when all the most difficult questions connected with locomotion are settled, the simple one discussed above is not satisfactorily determined. In consequence of the opinion of Muybridge we are unwilling to deny that the movement, though commonly beginning with a fore-limb, may be started by a hind-leg; nevertheless, in the experience of the writer and those who have observed for him, the movement invariably begins in front, and never behind, unless the horse is 'reining back.' The first step taken in walking backwards is always with a hind-limb, which appears to support the view that the fist step forwards is always made with a fore-limb. On the other hand, the first step in draught may be taken with either a fore or a hind leg; the former if the draught is easy, the latter when it is heavy. In 'backing' in draught a hind-foot is first moved if the load be light; if heavy, the animal leans well back and moves a fore-foot first. If the horse's head be placed uphill he starts with a fore-leg, provided the hill is not steep; if steep, he starts with a hind-limb. When the head is downhill the first step is taken with a fore-leg.

A fore-limb having initiated the movement, the next leg to take part is the diagonal hind; for instance, if the step begins with the off fore, as in Fig. 211 (1), the next leg to move is the near hind (2). This is followed by the near fore, and lastly by the off hind. There are four distinct movements in each stride of the walk, and as there are two strides to a complete advance of the body—viz., one on the near and one on the off side—there are altogether eight movements. The best method of conveying the eight movements of the walk is by means of a system of notation,* as in Fig. 212. This shows that in the walk the limbs on the ground at any one time are three, followed by two, followed by three, and so on. In Fig. 211, (1) shows that the support may be by means of one fore and both hind legs, or one fore and one hind diagonal, as in (2), or both fore and one hind, as in (3), or one fore and one hind lateral, as in (4).

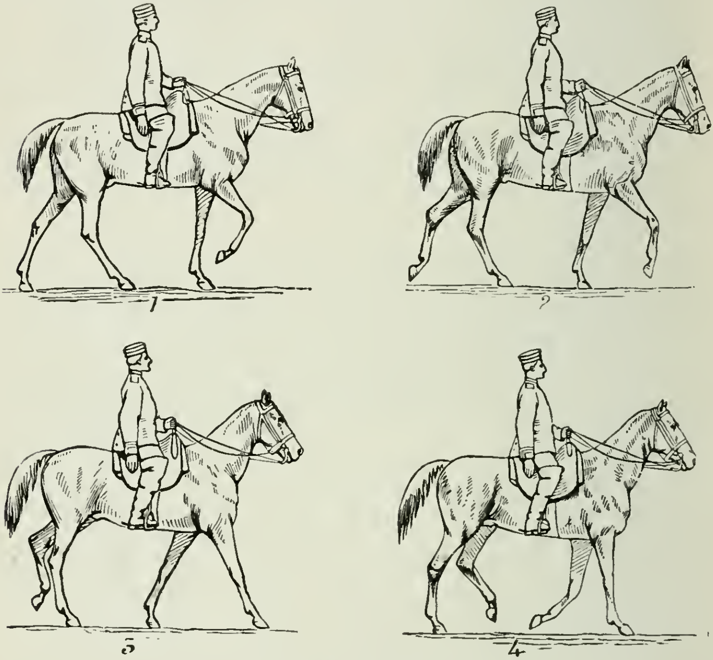

Fig. 211.—The Walk (Ellenberger).

There may be slight variations in the walk, such, for instance, as in the case of a draught-horse loaded or a horse out grazing; but in the true walk the broad principles above described are never departed from. In Fig. 212 may be seen some of the features of the horse's walk. It will be observed that the three limbs followed by two is the characteristic, the three limbs being any three, the two being any two, provided one is a fore and one a hind. The track left by a horse at the walk is shown in Fig. 224. If a track be studied, it will be observed that the impression of the hind-foot is generally in advance of that of its fore-foot, the limbs being in the position of the near legs in Fig. 211 (4). But there is considerable variation; the hind-foot in a good walker will always be placed down in advance of the impression left by the fore-foot. In an average walker the hind-foot impression covers the fore more or less; in a horse that is a bad walker, or is tired, or taking short steps for any reason, as in heavy draught, the hind-foot impression is behind the fore. In draught it comes behind the fore if the traction be heavy; in descending a hill, it comes behind the fore if the load is under control, but it falls in front of it if the weight cannot be properly held back. The fore-leg remains on the ground for a longer time than it takes in passing through the air, comprising the period during which the body is passing over the limbs. The movement in the air of both fore and hind legs is so extremely rapid as almost to defy detection. The snatching up of the foot from the ground is the quickest movement. Muybridge, following Gamgee (senior), refers it to the spring or rebound of the suspensory ligament, but it would seem to be due entirely to the flexor muscles.

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* In the diagrams of notation the narrow end of the figure represents the head; the spots represent the legs on the ground at any one moment; they do not, of course, represent the relative position of these limbs to each other.

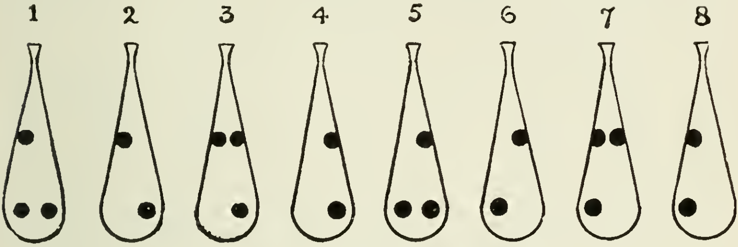

FIG. 212.—NOTATION OF THE WALK.

1, 2, 3, and 4, correspond to similar numbers in Fig. 211.

The writer caused horses to trace the movement of the leg from the time the foot left the ground until it returned. A pencil was fixed at right angles to the foot, and the horse walked past a piece of prepared canvas, arranged vertically, on which he traced the limb movements. There was a great deal of variation in the character of the curve, depending upon the part of the foot to which the pencil was attached, a toe curve being different from one taken at the quarter.

Fig. 213 shows two curves obtained by this method; they illustrate the sharp flexion of the foot, followed by a fall, and then a rise as extension occurred. The foot is at its greatest height from the ground in the middle of extension.

In A the stride was 4 feet 2 inches in length. There is a short upstroke, then a sharp curve upwards as the foot is flexed, followed by a fall; extension of the limb then takes place; this gives the long bold curve, until the ground is again reached. The foot was flexed 2 inches in height, but extension raised it 4 inches from the ground.

In B the stride is shorter; there are peculiar curves at starting which were very noticeable in many tracings, of which the actual cause is doubtful; it was thought they were due to an inward rotation of the limb. The rise in extension is well marked.

The curves are not to scale. They are exact reproductions of sketches made at the time (thirty years ago) in the writer's notebook.

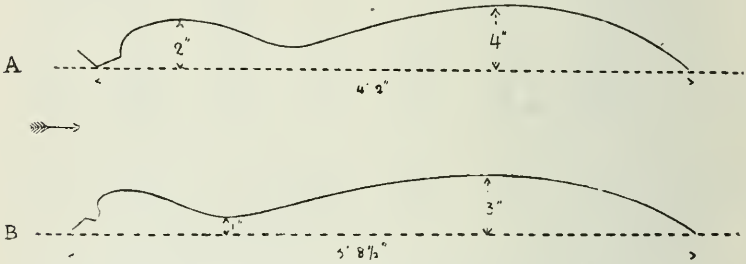

Fig. 213.—The Curve made by the Foot from the time it leaves the Ground until it again makes Contact.

The pencil was fixed at the quarter of the foot. The arrow shows the direction in which the horse is travelling; the dotted line represents the ground.

In walking on level ground the majority of horses rarely extend the knee any great distance beyond a vertical line dropped from the point of the shoulder. A sudden movement of the extensors now straightens the limb, and the foot is placed down flat. If the leg is not fully straightened by the extensor muscles, the foot comes to the ground toe first, with the knee slightly bent, and a stumble follows. In heavy draught-work it is no uncommon thing to see the toe put down first, but here the conditions are very different. Some horses walk with a pair of lateral legs, both off and both near alternately. The camel employs lateral legs as a natural means of walking. All horses in walking nod the head as each fore-limb advances; it is the only pace in which this occurs. The nod takes place at the moment shown in Fig. 211 (1).

The walk is a most important pace; few horses are capable of walking well, but it can be greatly improved by education. The ordinary saddle-horse has a *stride* of from 5½ to 6 feet (1·67 to 1·83 metres) at a walk. A *step* made either by a pair of fore or a pair of hind legs varies from 33 inches to 39 inches in length (0·84 to 1 metre).

The Trot.

A trot may be described as slow, ordinary, and flying. In the last there is a slight difference in the support given the body, but in the other two the movements of the limbs are identical. The trot is a very simple pace to observe, inasmuch as the legs are worked in pairs, so that instead of four moving in different times, there are two moving together. The two are *diagonal* legs, one fore and the opposite hind. These thrust the body forwards off the ground, and it is received on their fellows, which repeat the movement. During each thrust there is a period during which the body is in the air and no legs on the ground. In the trot there are two steps to the stride, and two periods in each stride that the horse is in the air; the steps are always with diagonals, as shown in the notation in Fig. 214. In Fig. 215 some of the characteristic phases of the trot may be seen. In (1) the horse is on diagonals; in (2) he has propelled the body forward and off the ground; in (3) the animal has alighted on the opposite pair of diagonals; and the process is then repeated. In America the flying trot has long been cultivated, with the result that some remarkable velocities have been obtained. The limb movements are not quite the same in the match-trotter as in the ordinary trotter. Muybridge shows it as follows (Fig. 216). The difference between match and ordinary trotting is that the match-trotter does not leave the ground simultaneously with a pair of diagonals, but with one at a time, nor does he arrive on the ground with a pair, but with one at a time. The interval in time between the arrivals is extremely small, but it distinguishes the flying from the ordinary trot. In the ordinary trot, it will be observed, the body is propelled by a

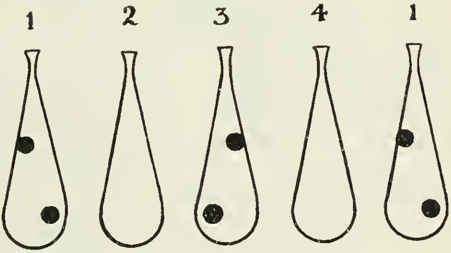

Fig. 214.—Notation of the Trot.

In (1) the body is being propelled by diagonal legs; (2) the body in transit and off the ground; (3) it is received by opposite diagonals, and again propelled.

diagonal fore and a hind leg simultaneously, but in the match-trotter the propelling is done first by a fore and then by a hind. This action of the hind-legs as propellers is important to notice; it does not occur in either the canter or the gallop, but appears again in the jump. It will also be noticed that the body, on coming to the ground, is received first by a fore and then by a hind limb. In the ordinary trot it is received by fore and hind limbs simultaneously.

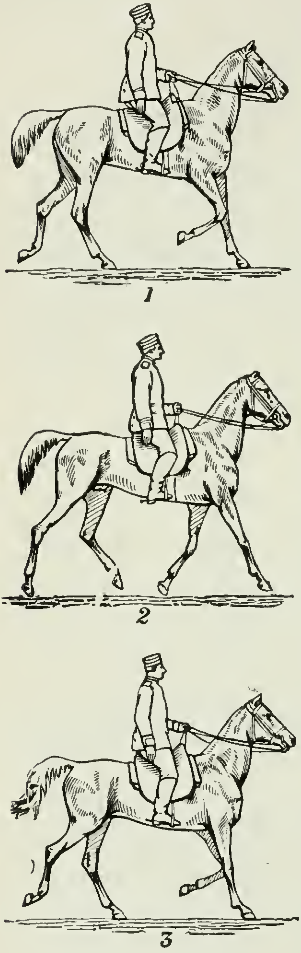

Fig. 215.—The Trot.

From instantaneous photographs by O. Anschütz (Ellenberger).

The velocity trotting horses attain is quite remarkable. The historic horse Edgington, the first to be photographed while moving, and whose stride when exhibited on paper revolutionised the public conception of animal locomotion, was taken while trotting the mile in two minutes sixteen and one-fifth seconds.[*] The length of the stride was 17 feet (5·15 metres), and the space traversed during the time the body was travelling through the air with no feet on the ground — viz., the period of suspension—was $5\frac{1}{2}$ feet (1·65 metres) at each step. This may be compared with the ordinary saddle-horse, which has a *stride* at the trot of 9 feet more or less. The length of a step taken either by a pair of fore or hind legs rarely reaches 5 feet, and is generally about $4\frac{1}{2}$ feet in length. The foot-tracks made on the ground by a horse trotting are shown in Fig. 224. In the trot the impressions of the hind-feet are generally made over those of the fore, but not always, as may be seen in the case of the off fore in the figure. The only real difference between the tracks of the horse trotting and walking lies in the interval between the feet—*e.g.*, in the length of the step and stride. The height of suspension in the air is greatly exaggerated in the trotting horse. In the ordinary horse it may scarcely be noticed, the feet being lifted only sufficiently high to prevent them being dragged over the surface of the ground. The distance covered during suspension is that which separates the fore from the hind legs; if these are between 3 and 4 feet apart, that is the distance covered while the animal is in the air. This will be realised from an inspection of Fig. 215 (2), in which the body is shown suspended, having just been propelled by the united actions of the near fore and off hind. The off fore and near hind are coming to the ground, and we know from our study of the foot-tracks that the latter will be placed over the spot just occupied by the near fore-foot.

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[*] Higher velocities than the above are common in American racing. The mile has been done in less than two minutes

When a horse falls at the trot, he does so either through not flexing his knee sufficiently before bringing the leg forward, or because the extension of the knee is not perfect, and in consequence the limb is unfit to stand weight. The knee should be sufficiently but not unduly bent, and the leg brought rapidly forward; the limb is then sharply extended, well braced, and the foot placed firmly on the ground heel first. Regarding the latter point, the question of pace settles whether the heel is distinctly first to make contact. In photographs of the match-trotter the inclination of the toe upwards as the foot comes to the ground is very marked. In slower trotting the foot comes down flat, but always with an inclination for the heel to make the first contact. When a horse is inclined to come on to the toe instead of the heel, which occurs when the muscles tire, when the feet are too long, or when the mobility of the joints is impaired, he at once stumbles.

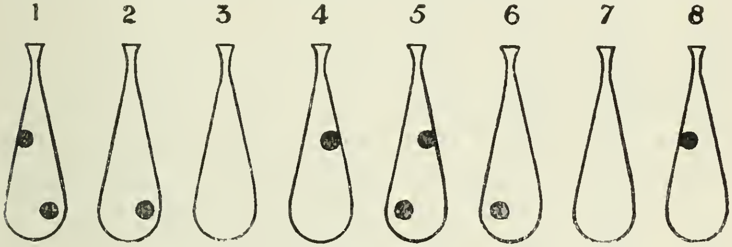

FIG. 216.—NOTATION OF AMERICAN TROTTING HORSE.

(1) The diagonals are preparing to propel; this is effected first by a fore-leg, one hind being left on the ground (2); the thrust from this lifts the body off the ground (3); it is then received on one fore-leg (4), and then by the diagonal hind (5). From this point the movement is a repetition of (1).

The **Amble** is the nearest approach to a run; it consists of a short, quick series of steps, in which lateral and diagonal legs are alternately employed, with no period of suspension—*e.g.*, there is no period during which the body is left without a leg on the ground. It is best studied from the notation in Fig. 217, which shows that it is executed by a pair of laterals, followed by a single fore lateral, succeeded by a pair of diagonals, followed by a single hind-leg and then a pair of laterals. From the fact that there is never a period during which the body is without support, the pace is an easy one for the horse; and as there is no thrust upwards into the air, it is an especially easy pace for the rider, who barely moves in his seat.

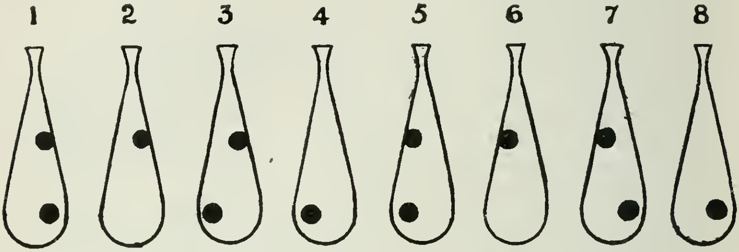

Fig. 217.—Notation of the Amble.

In **Pacing** or **Racking** the horse, instead of using diagonal legs, uses the lateral limbs, so that off fore and off hind are on the ground instead of off fore and near hind (see Fig. 218). An animal may 'pace' both at the walk and at the trot, in this respect resembling a camel. There is no doubt that it is a perfectly natural movement for some horses; others are taught it. Some extraordinary velocities are recorded in America in this gait. In fast paces the horse oscillates from side to side; the appearance is very unsightly, and racking is not encouraged in preference to trotting. A defective leg which will not stand trotting may stand 'racking.'

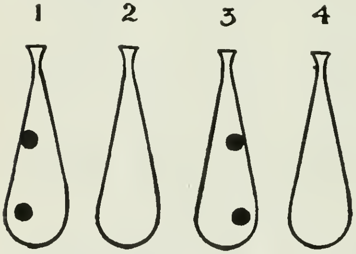

Fig. 218.—Notation of the 'Pace' or 'Rack.'

The Canter.

This is a pace entirely different from any previously considered. To understand the canter clearly, it must be remembered that the body is propelled forward by one fore-leg, and no matter which of the two it may be, it is received on coming to the ground by the opposite or diagonal hind-leg. There is no exception to this rule, which will be found equally true for the gallop. It is well to get this fact clearly established (see Fig. 220).

In (1) the animal is propelling the body off the ground with the off fore-limb, and in (3) alights on the near or diagonal hind-leg. The importance of the principle of the employment of diagonal legs will be observed; we have seen it in the walk, it is the essential feature of the whole movement in the trot, and we now meet with it in the canter. The notation of the canter is shown in Fig. 219. It starts from the moment the body is in the air (1), where it has been propelled by the leading fore-leg*—in this case the near. The animal alights on one hind-leg, the off (2), the diagonal to the leading fore-leg; this is followed by the fore-leg on the same side—viz., the off—coming to the ground (3), so that for a very brief period the body in the canter is supported by lateral legs. The next change is that the fellow hind-leg comes to the ground (4), the body now being supported on one fore and both hind limbs; the hind-limb which first received the weight is then withdrawn (5), and the animal is left on diagonals. This is followed by the leading fore-leg coming to the ground (6), so that the body is now supported on both fore-limbs and one hind-limb. The off fore-limb is next withdrawn, and the animal is left on lateral legs (7); the near hind is withdrawn, and the horse left on one fore-leg (8), which, as we have seen, is the leading or propelling limb. This sounds very complex, and there is no doubt that the canter is difficult both to analyse and describe. It will be observed that in the seven sequential movements of the canter the body is twice—viz., at the beginning and end of the movement—on one leg; at two periods it is on two lateral legs; at two periods it is on three legs; and at one period on diagonal legs.

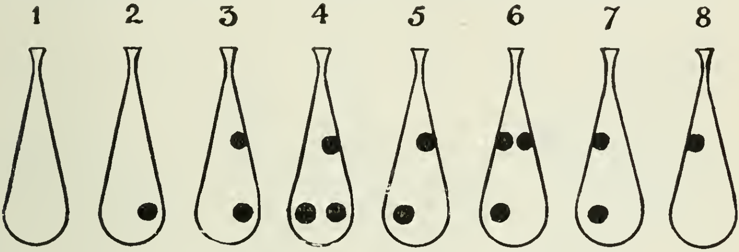

Fig. 219.—Notation of the Canter.

Turning now to actual photographs of these movements, we see in Fig. 220 (1) the propulsion from the ground by means of the off fore-leg; (2) represents the animal in the air; (3) shows the horse alighting on the near or diagonal hind-leg; (4) exhibits the animal standing on two lateral legs, the off hind, it will be observed, not yet having reached the ground. In (5) the body is on three legs, both hind and near fore; in (6) the animal is on diagonal legs, near fore and off hind only: the toe of the near hind is just leaving the ground. Had the picture been taken the merest fraction of a second later, this foot would have been

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* The leading fore-leg in the canter and gallop is the one which gives the final propulsion; it is the leg which does all the work. When going straight, either fore-leg may lead, and a well-trained horse should be taught to save leg weariness by changing the leading leg. In turning or moving on a circle to the left, the leading leg must always be the left; similarly, in circling to the right, the leading leg must be the right.

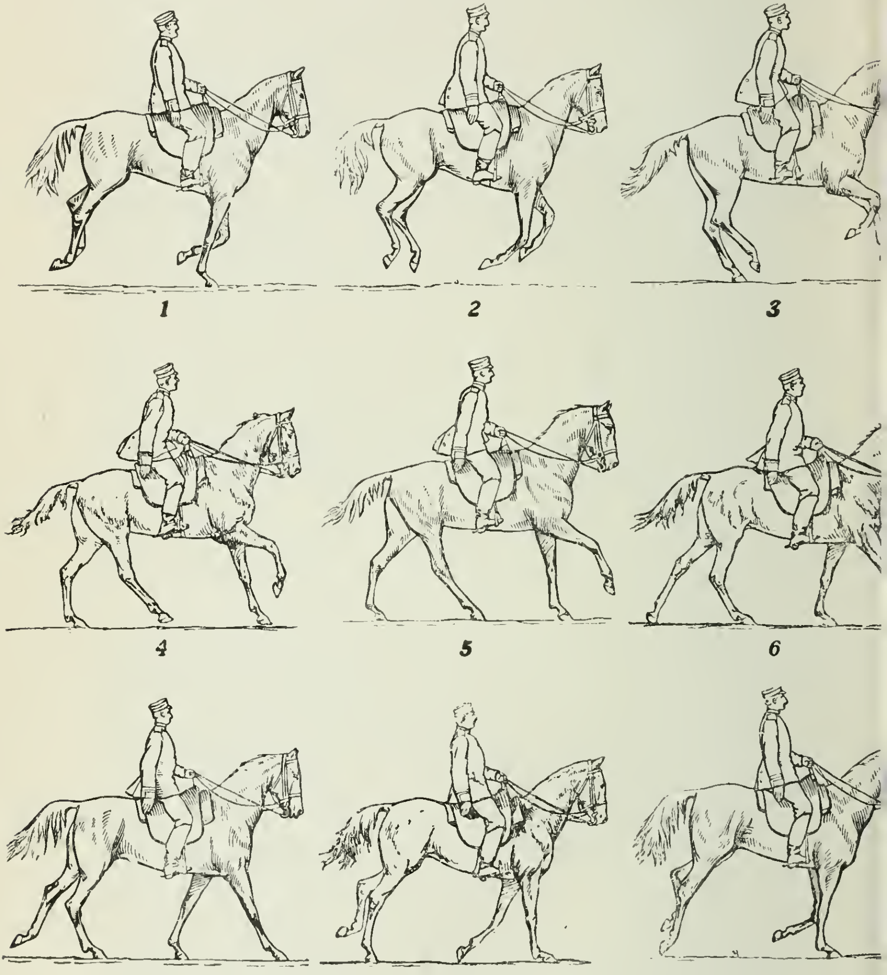

FIG. 220.—THE PHASES OF THE CANTER (ANSCHÜTZ).

seen off the ground. The animal, however, is clearly on diagonal legs, for a hind-leg thrust as far back as that shown in (6) is of little support. In the next figure (7) the off fore-leg has come to the ground, and the horse is standing on three legs. Of these, first the near fore (8) is snatched up, leaving the body balanced on lateral legs, followed by the off hind (9), which leaves the animal on one fore-leg, the off, preparatory to the final spring, which is farther advanced in (1), and actually occurring in (2).

The canter is an easy pace for the rider, owing to the number of limbs supporting the body in turn—as many, in fact, as in the walk; it is this which gives smoothness to the working. To obtain smoothness the limbs must follow in definite order. A horse that can canter only with the off fore leading is anything but comfortable when he tries to lead with the near fore; it is impossible for him to group his legs in the correct order—everything is disjointed owing to want of proper co-ordination. To learn to lead freely with either fore-leg should form an essential part of the training of every saddle-horse. In this way he will change as one leg tires, and so save himself from a sprained limb.

The essential features of the canter being a hind-step, a fore-step, and a spring, it is desirable to glance at the value of these in an ordinary horse. The step with a pair either of fore or hind legs varies from 37 to 43 inches in length. The stride varies from 9 feet 8 inches to 11 feet 8 inches. The difference in the length of the stride does not depend so much on variations in the length of the step as in marked variations in the distance of the spring. In a slow canter the spring may be half a foot or even less, whereas in a fast canter it may be 2 feet or more. The tracks left by a horse cantering are shown in Fig. 224. The length of this horse's stride was 10 feet 8 inches, and the spring forward was 6 inches.

The Gallop.

Muybridge points out that all animals do not gallop alike—that is to say, by means of identical leg movements—nor, in the case of the dog, does the same animal always gallop in the same way. There are two distinct gallops described by Muybridge: one he calls the *transverse*, the other the *rotatory* gallop. In Fig. 221, A, the scheme of a transverse gallop is shown; in B that of a rotatory gallop. The horse always employs the transverse, while the dog and many other animals use the rotatory gallop.

To understand the gallop it is essential to remember that the propulsion or spring is done by one fore-leg, and, as in the canter, the body alights on one hind-leg, which is always the diagonal one to the propeller. The body, having alighted, a step is made with the hind-legs, then a step with the fore-legs, from which it is again propelled. As in the case of the canter, there are two steps and a spring in the stride. There are seven different positions assumed by the legs during the gallop, which may be seen in Fig. 222. Beginning with the body in the air, as in (1), the animal alights on one hind-leg (2), in this case the near, as the leading leg was the off. This receiving leg is thrust well forward under the body, in great contrast to its position in the canter, and for a minute period the animal is standing on one leg; the opposite hind-leg then makes a step and comes to the ground (3); the body is now momentarily on two hind-legs. The fore-legs have not yet reached the ground; they are being advanced as far as possible to the front, and to enable them to reach forward the first hind-leg is snatched off the ground, and the animal is again left standing on one hind-limb (4). The fore-legs now begin their descent, and the one diagonal to the hind-limb on the ground now makes contact (5). The horse's body is then supported on one fore and one hind diagonal legs. It is now the

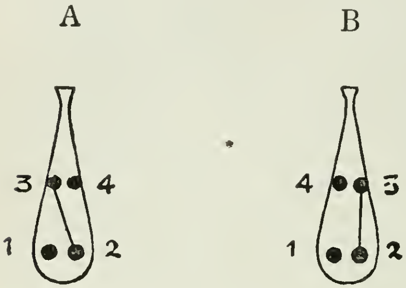

FIG. 221.—SCHEME OF THE GALLOP.

A, Transverse gallop; the legs move in the order of the numbers. B, Rotatory gallop.

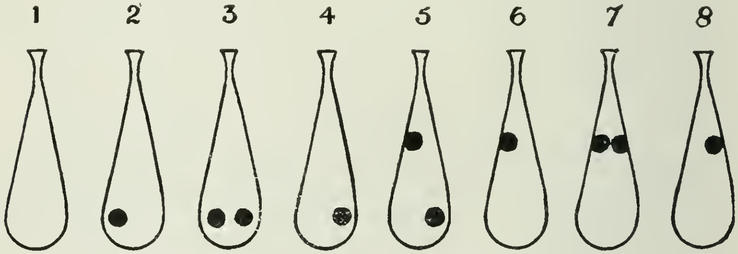

FIG. 222.—NOTATION OF THE GALLOP.

turn of the fore-legs to make their stride, and to effect this the body rotates over the fore-leg, and in doing so the hind-leg leaves the ground. The animal is once more left on one leg (6). The step is now made, both fore-legs being on the ground (7); the first fore to reach the ground is now snatched up, and the horse is left standing on one leg (8), which is the leading one, and within the next fraction of a second the body is in the air. In Fig. 223 each of the important movements is shown in the horse. (1) is the body in the air; the manner in which the legs are collected under it should be particularly noted; the hind-limb which is about to make contact is thrust as far forward as possible. In (2) this limb has reached the ground; in (3) its fellow has arrived, and the step with the hind-legs been taken; in (4) the big reach forward has occurred, to effect which one hind-leg has been withdrawn; in (5) the body is rotating over one fore-leg in order to make the step with the fore-legs; at (6) this step has nearly been effected; at (7) the step has been taken, and the fellow-fore-leg withdrawn; the body has now rotated over the leading leg at (8), and when this has been completed the spring into the air is made. The gallop is an easier pace to follow than the canter; there are never more than two legs on the ground at any time, and the greatest part of the work is done by one leg. Briefly, a hind-step with no support in front, a fore-step with no support from behind, and a spring, constitute the essential features of the movement. The only time when the hind-leg gives any assistance to the fore-limbs is when one of the latter makes the forward reach preparatory to taking its step. When a horse gallops, no matter how fast, the fore-feet never extend in front of a vertical dropped from the muzzle. In Fig. 224 is shown the track left on the ground by a galloping horse. Muybridge, working with an average thoroughbred in racing condition, galloping at the rate of thirty-five miles an hour, obtained the following results: Length of stride, 22 feet 10 inches, made up as follows:

Fore-step - - - - - -	5	feet	0	inches.
Hind-step - - - - - -	3	,,	10	,,
Interval between hind and fore legs -	7	,,	6	,,
Spring - - - - - -	6	,,	6	,,

With the ordinary horse, the strides of which vary from 15 feet to 19 feet, the following results were obtained:

Fore-step - - -	3	feet	5	inches	to	4	feet	3	inches.
Hind-step - - -	2	,,	11	,,	to	3	,,	11	,,
Spring - - -	2	,,	11	,,	to	6	,,	2	,,

Here, again, it was shown that the difference in the length of the stride is due not so much to difference in the length of the step as in the distance of the spring. The forward reach, such as the horse is making with the off fore in Fig. 223 (3) is of much the same length in all ordinary animals—viz., 5 feet 5 inches to 6 feet—though occasionally as much as 6 feet 6 inches. In the race-horse above referred to it is 7 feet 6 inches. It will be observed that both in the race-horse and the ordinary horse the

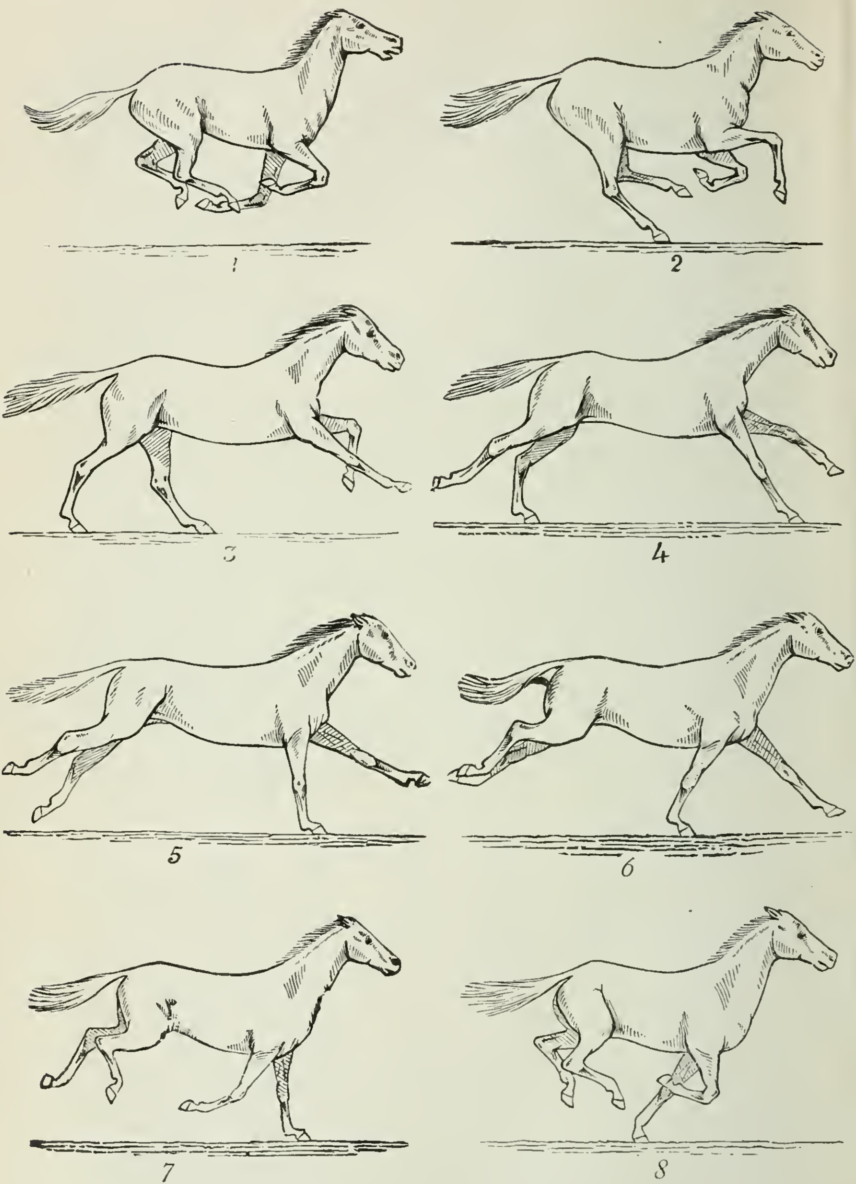

FIG. 223.—THE PHASES OF THE GALLOP.

After Stanford, Muybridge, and Stillman ('The Horse in Motion').

step taken by the fore-legs in the gallop is longer than that taken by the hind-legs. For the velocity of the gallop see p. 698.

Differences between the Canter and Gallop.—In the canter it can be seen that the horse makes a big step first with the hind-legs, then with the fore, followed by a spring; he is only once in the air in each stride. In the gallop the same essential features occur; but the canter differs from the gallop in being a slower pace: the hind-leg, in order to receive the weight, is *not* brought well under the body (see Fig. 220, 3), and in consequence, to enable the hind to complete its step, the lateral fore-leg has to come to its assistance. There is no such support given with a fore-leg in the gallop. In consequence of the slowness of the canter, one hind-leg has now in turn to help support the body while the fore-legs make their step, and this support is not withdrawn until the one fore-leg is ready to make its spring. No such hind support exists in the gallop during the period the fore-legs are making their step. In the gallop there are never three legs on the ground at one and the same time; in the canter this occurs twice in a single revolution.

The conventional gallop shown in pictures is much more pleasant to look at, but wholly incorrect. F. Galton* observed that the two fore-legs in the photographs of the gallop were extended during one-quarter of a complete motion, and during another quarter the two hind-legs were similarly extended; cutting the photographs in halves, and uniting the front half of the former to the hind half of the latter, a fair equivalent of the conventional attitude was obtained. He believed that, owing to the confusion created by the limb movements in the gallop, the brain ignores one-half of all it sees, divides the other half into two parts, each alike in one particular, and then combines the two halves ' into a monstrous whole.'

The **Gallop of the Dog** is rotatory, as Muybridge terms it (Fig. 221, B), and the greyhound gallops differently to a heavy dog. The latter employs the gallop of the horse, excepting that the animal alights on the lateral and not on the diagonal hind-leg; the opposite hind-leg then comes to the ground, next the fore-leg of that side, then the opposite fore-limb, followed by the spring. The order is, therefore, as follows, assuming the thrust is given with the left fore-leg: left fore, left hind, right hind, right fore. As in the horse, there is a step with the hind followed by a step with the fore legs, then a spring. The movement of the limbs of the greyhound also follows in the order: left fore, left hind, right hind, right fore; but there are two periods of propulsion, first with a fore-leg, which sends the body into the air with the fore and hind legs crossed like a pair of scissors, next a thrust with a diagonal hind-leg, which shoots it once more into the air, to alight on a lateral fore-leg. Consequently, in a single stride of the greyhound there are two springs, once from a fore-leg and once from a diagonal hind-leg.

The **Footprints** occurring during the various paces of the horse have been previously referred to; they are illustrated in Fig. 224. Before the days of instantaneous photography a great deal of attention was paid to them as a graphic record of locomotion, and nothing, perhaps, better illustrates how differently horses move while performing the same pace, or even the same horse at different times. The differences do not, of course, lie in the modes by which the limbs are moved, but in the length of the steps taken and the position of the feet relative to the central line of the body. In the walk, for example, the hind-feet may be placed down immediately on top of the impressions of the fore, or they may be placed in front of or half covering the fore-prints. The only real interest now attached to a study of footprints lies in the information they furnish of the extent to which the feet are brought under the middle line of the body as a means of support. This is ascertained by the use of a line so adjusted as to lie midway between the tracks made by the near and off feet. Such a line represents the middle line of the body. It might at first sight be reasonable to suppose that the off feet would fall to the right and the near feet to the left of such a line, and that the distance the impressions were made from the central line would be similar to their distances from a line passing midway between the feet during repose. But this is not so; a pair of fore-feet 5 inches apart during repose may be shown during locomotion to be brought completely under the middle line of the body, or even to cross it. During the slowest paces the feet are planted very nearly or quite in a line with the centre of the body; during the faster paces they may be brought so far under from either side as to cross the central line. In the gallop the feet are brought well under the central line of the body, forming a very straight track, occasionally broken by their being planted away from the centre, or their sometimes completely crossing the centre to the opposite side of the body. All the features discussed may be seen on inspection of the various foot-tracks shown in Fig. 224. The dotted line represents the middle line of the body.

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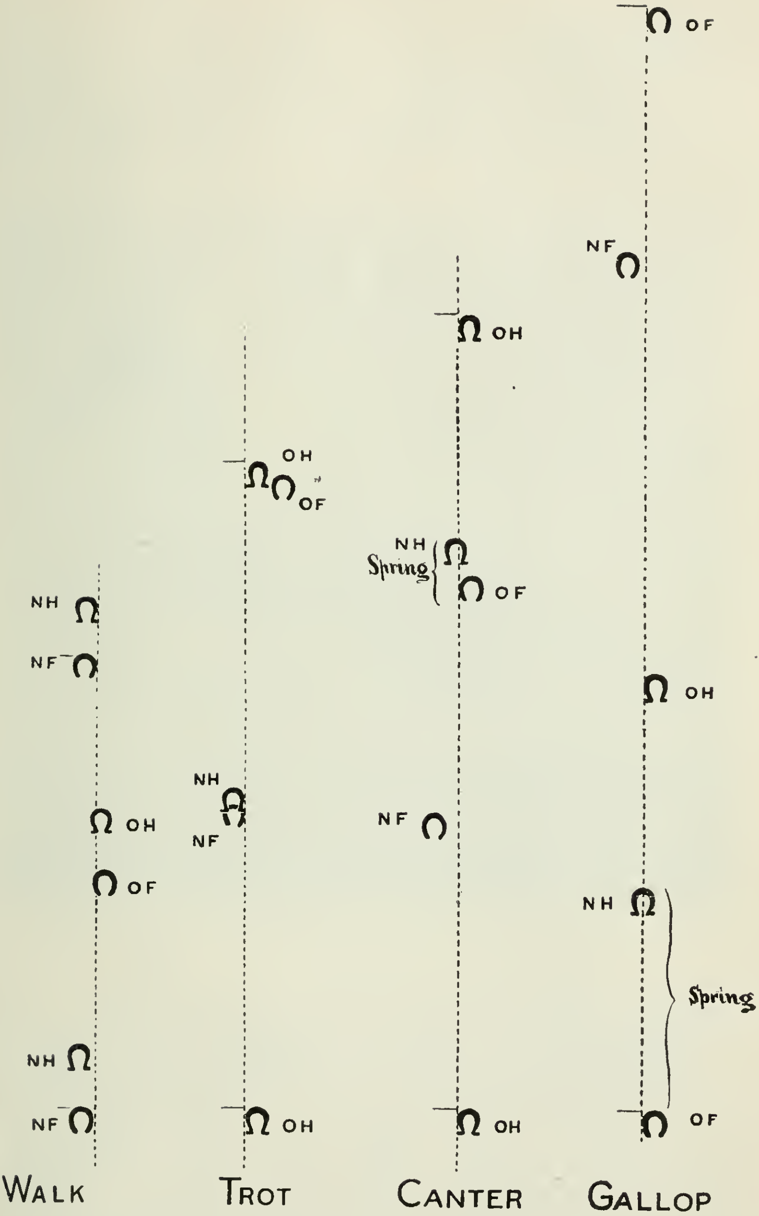
* ' Memories of My Life,' 1908.

Summarising these results, we see that, though in repose the feet may be 4 or 5 inches apart measured from their inside edges, the tracks these feet leave on the ground do not show this interval; on the other hand, they are brought well under the centre of the body, sometimes even crossing it, and the faster the pace, the nearer the footprints approach a straight line. It is obvious that the more the feet are brought under the middle line of the body, the more stable the support afforded, but it is not clear how they are able to avoid striking their fellows.

The Jump.—It is said that no two horses jump alike, and even that the same horse under identical conditions will jump differently. The differences alluded to originate in the manner in which the hind-legs are disposed preparatory to the body being collected for the spring upwards. Under ordinary circumstances, as the jump is approached, the animal is steadied in his stride, in order to afford him the needful opportunity of ‘collecting’ himself and forming his judgment of the obstacle. During the steadying period he is getting ready to raise the fore-hand; this he could not properly effect without a modification of the pace; he is also estimating at what point he should take off. This has to be learnt by experience; everything depends upon it. In Fig. 226 (1) and (2), the horse is seen steadying himself, bringing the hind-legs well under the body, and raising the fore-hand. In (3) the final upward push has been given by a fore-leg, and in this process not only the fore-legs, but the muscles of the back and loins, are playing a most important part. It is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OF
WALK
TROT
CANTER
GALLOP

FIG. 224.—FOOT-TRACKS AT VARIOUS PACES.

A stride is indicated by the line at the toe of identical feet. These tracks were furnished by the same animal.

impossible for a horse to rear even to the partial extent required for an ordinary jump if the back is weak. In (3) the obstacle is being faced, the animal is lifting the fore-hand and bending the knees, the hind-legs being well under the body, in order to support the weight. The next important point is the continued bending of the knees in (4) and the straightening or extension of the hind-legs. The moment the fore-feet are above the level of the obstacle, propulsion forward with the hind-legs begins; first both hind-legs straighten themselves, extending to the utmost, while the limb nearest the jump is left to give the final push off (5) and (6). It is now the turn of the hind-legs to become flexed, the hocks bending as much as the knees had previously done, while at the same time the fore-legs now extend, with the object of making contact with the ground. This contact must be made with a firm, straight leg, one (6) followed by its fellow (7), which in (6) is seen placed out in advance. It is advanced in order that the first fore-leg to make contact (6) may be carried forward out

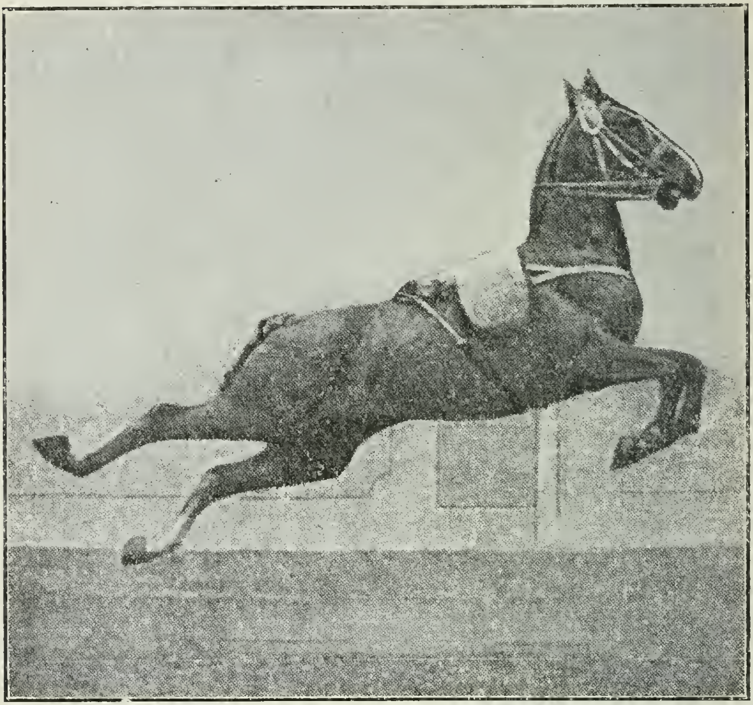

FIG. 225.—A JUMP WITHOUT AN OBSTACLE BY A HIGHLY TRAINED ANIMAL.

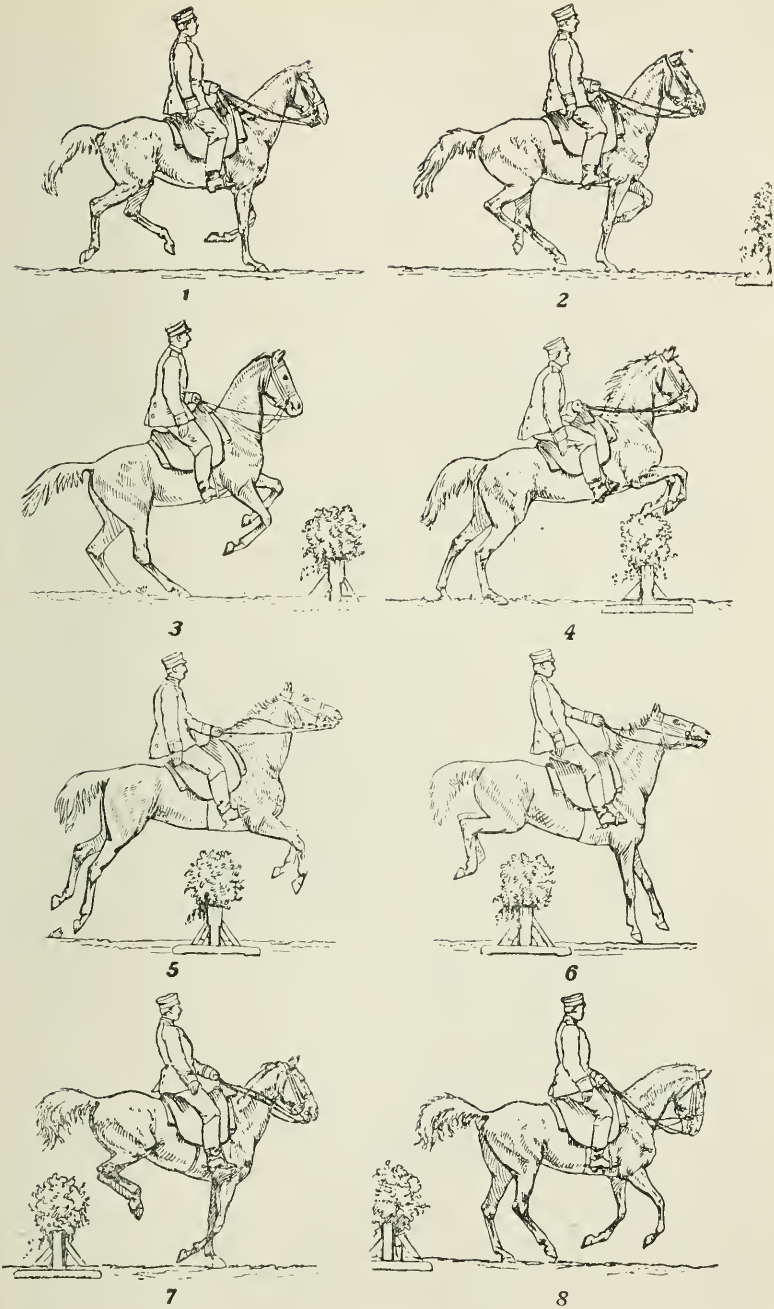

Fig. 226.—The Phases of the Jump (Anschütz).

of the way (7), for it is occupying the place where the hind-feet will alight. These now come down, first one, then its fellow, but before the second hind-leg reaches the ground the fore-leg has already pushed off (8). It will be observed that the jump resolves itself into a partial rear, a doubling up of the fore-limbs and powerful extension of the hind, followed by the upward push, the extreme flexion of the hocks, the marked extension of the fore-legs, and the reception of the weight of the body on first one and then the other fore-leg. Should the animal fail to alight fair and true on his fore-feet he falls, generally pitching on to his head. The jump reverses the use of the limbs in ordinary locomotion; there the thrusting is done by the fore-legs, and the weight of the falling body is received on the hind; in the jump the hind-legs do the thrusting and the fore-legs receive the weight of the falling body.

A record jump is believed to be that of 'Confidence' at Olympia in 1912, when 7 feet 5½ inches were cleared. A jump of 25 feet without an obstacle has been recorded. A brook of 19 to 21 feet in breadth has been known to work havoc with such a hunt as the Pytchley. Fig. 225 shows the attitude of a highly trained horse in making a jump without an obstacle.

In **Kicking** with both hind-legs (Fig. 227) the head is depressed, a powerful contraction of the muscles of the quarters and back, A A, throws the croup upwards, the hips are flexed through B B, the stifles by the contraction of C C, and both legs are violently extended through D D. No estimate of the force employed in kicking can be made. A shell is not productive of more damage than that caused by a determined kicker. It is no figurative expression to say that under suitable conditions the muscles may he heard to contract. Kicking may be practised either with both hind-legs backwards, or with one hind-leg backwards, forwards, or outwards. The two latter methods are very dangerous; fortunately, few horses can effect them. Owing to the presence of the pubo-femoral ligament, a horse can kick outwards only with difficulty. It is known as 'cow-kicking,' but this term may also be applied to the forward kick. Striking with the fore-feet and cow-kicking are not common among nor characteristic of British horses; they are methods of attack particularly employed against man.

It is rather remarkable, however, that our horses should be so much more given to kicking among themselves than those of Continental nations.

In **Rearing** (Fig. 228), the fore-hand is raised by the centre of gravity being thrown back, and by the body being pushed upwards by the fore-limbs, and at the same time raised by a contraction of the long muscles of the back (A B) which run from croup to neck, attached throughout their whole length to the vertebræ (Fig. 229). The muscles of the hind-limbs keep the

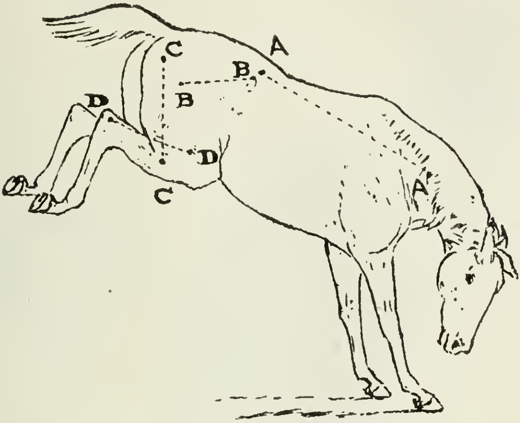

FIG. 227.—KICKING (AFTER PEYREMOL).

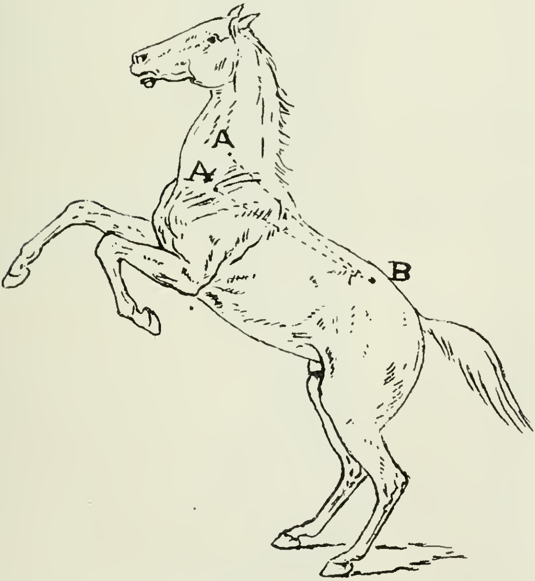

FIG. 228.—REARING (AFTER PEYREMOL.)

stifle-joint closed, and the hock-joint open, without which provision the extra weight would cause the animal to sit down. The position in Fig. 228 is one of perfect stability. More

1 and 8, *ilium* ; 4, spinous processes of dorsal vertebræ ; 2, 3, 5, and 6, *Longissimus dorsi*, 6 being the portion known as the *semispinalis*, 7, *Ligamentum nuchæ* ; 9, *transversalis costarum*.

The longissimus dorsi is the largest and longest muscle in the body. When the head is raised, it acts from behind forwards, and pulls the neck and body farther back as in rearing. When the head is depressed, it acts from before backwards, and raises the croup and loins as in the act of kicking (Fig. 214). In consequence, if a horse's head is kept raised, he cannot kick with both hind-limbs.

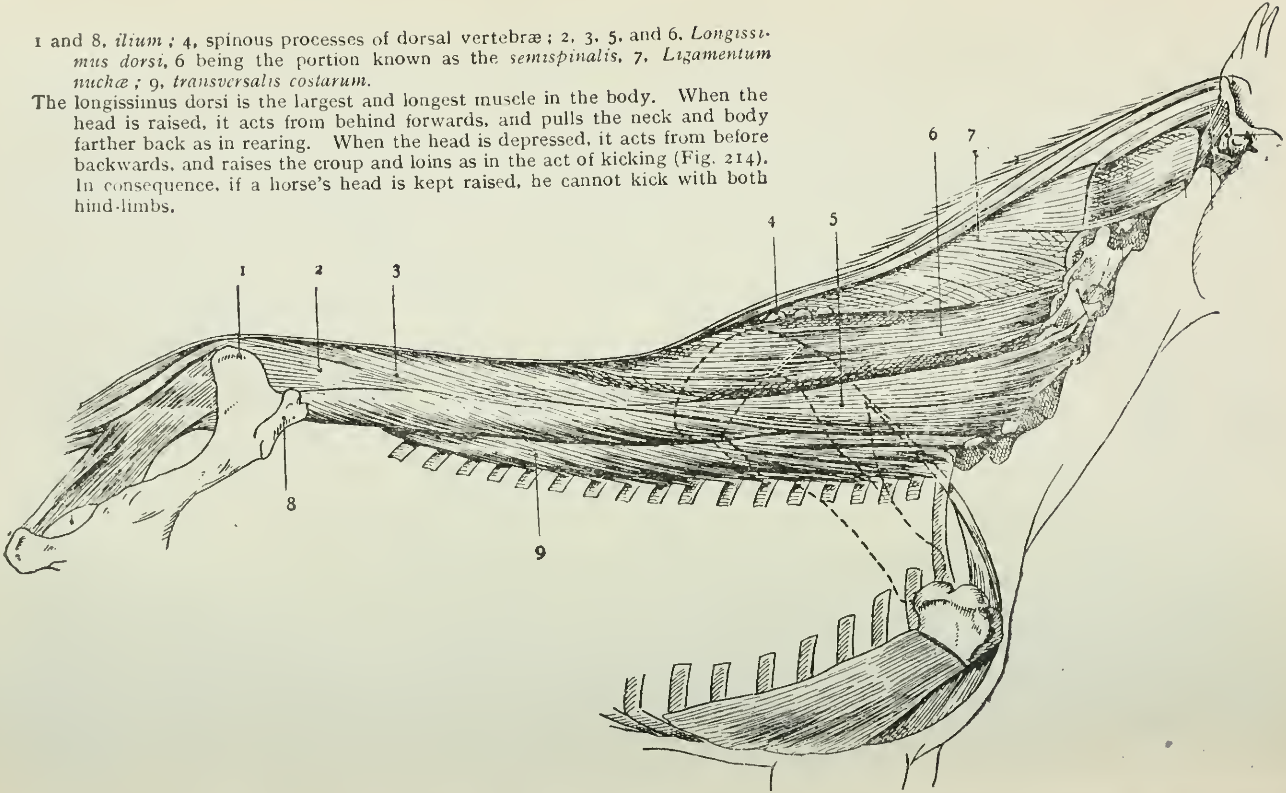

FIG. 229.—MUSCLES OF THE BACK AND LOINS (ARMSTEAD).

powerful contractions of the muscles inserted into the cervical vertebræ will pull the body farther back, and if it passes outside the base formed by the hind-feet, the animal comes completely over, either on to its side, or frequently on to the occiput when rearing through temper. A fall on the occiput commonly results in a fracture of the base of the skull.

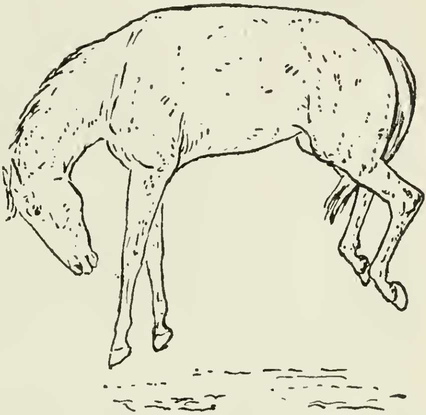

Fig. 230.—Buck-Jumping (after Peyremol)

In **Buck - Jumping** (Fig. 230) the animal springs bodily and suddenly off the ground, the head being depressed between the fore-legs and the back violently arched. In this action the psoas muscles play an important part by bending the hind-quarters inwards, but they cannot by themselves produce the arched condition of spine, which largely depends, apart from the upward spring, upon the ability to get the head down, the neck bent, and the abdominal muscles firmly contracted. Much the same configuration of spine occurs when horses are cast for operation, and in practice this is controlled by keeping the head and neck straight, and the tail from being forcibly drawn in (see p. 446). In buck-jumping it is the spring which displaces the rider.

SECTION 3.

Work.

The **Amount of Work** expected from horses is a question which has hitherto been greatly lacking in exact expression. That many animals are worked beyond their powers is undoubted, the evidence being the short duration of their useful life. In days gone by, when the horse was the only means of transport, there was no attempt made to save him, especially in public vehicles; his life in the early stage-coach was three years. The stages were from fourteen to twenty miles in length, but experience and economy brought them down to ten miles, with a rest on the fourth day. Youatt* tells us that towards the end of the eighteenth century, during election-time, bets were made as to which express would kill the greatest number of horses.† In his day animals in the public omnibuses only lasted five or six months. Taplin, writing in 1793, says that the rage for expeditious travelling was leading to the destruction of thousands of horses. In an otherwise admirable book on horse management, published in 1805,‡ it is stated that a horse should travel thirty to forty miles on end without drawing rein at from eight to ten miles an hour; this is described as ordinary work! Severe or, as it is termed, 'extraordinary' work was represented by a gallop of twenty miles, or trotting sixteen miles in the hour. W. Ward,§ in 1776, advised that a distance of forty-five to fifty miles a day in three stages should not be exceeded. He says he knew of people doing sixty, seventy, and eighty miles a day, but it required a very good horse, and could *only* be done for one or two days. J. Lawrence, writing in 1809,‖ considered that fifty to sixty miles a day, between 7 a.m. and 5 p.m., could be done in stages of twenty miles, trotting and cantering alternately. In a journey lasting weeks and months together, he regarded twenty to thirty-five miles a day as suitable. The ordinary hack of that period is described as travelling forty or fifty miles a day at seven or eight miles an hour, and it is stated that with a suitable weight they may do this for two or three successive days. The best hack did ten or eleven miles an hour, and anything over sixty miles a day was considered 'a severe trespass on their powers.' These facts are mentioned in order to explain that the general feeling during the eighteenth century was in the direction of excessive work, the racing especially being of a most punishing character. When Watt, who presumably knew nothing of horses, was determining the working power of his engine, he adopted a standard known as 'horse power,' which has ever since been misleading. He found that a horse could raise a weight of 150 pounds passed over a pulley at a rate of 220 feet a minute (equal to 2½ miles an hour): 150 × 220 = 33,000 pounds lifted 1 foot high per minute, or 33,000 foot-pounds per minute. From that time, on the basis of Watt's original excessive estimate, the most extravagant demands have been made on the strength of horses, for which engineers and mathematicians, who alone have studied the question, have been responsible. A horse can, of course, raise 150 pounds at the velocity mentioned, but the practical question is for how long? He could do it for three and a half hours and not be overworked, but eight actual working hours are expected from him, and the standard then becomes excessive. Horses ploughing frequently exercise a force of 150 pounds, but here the pace is the saving factor.

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* 'The Obligation and Extent of Humanity to Brutes,' 1839.

† In the *Gentleman's Magazine* for 1825 it is stated that a stage-coachman admitted to having killed fifty horses in one year from overdriving.

‡ 'Analysis of Horsemanship,' Adams.

§ A 'New Treatise on the Method of Breeding, Breaking, and Training Horses.'

‖ 'History and Delineation of the Horse.'

The question of condition or fitness for work is discussed at p. 447.

Mechanical daily work is the product of three quantities—the *effort*, the *rate*, and the *number of working hours*. The difficulty lies in determining the effort; there is no means of ascertaining this with any degree of precision in riding-horses, but with draught animals by means of a dynamometer it can be registered with sufficient accuracy. It is evident, however, that the force of traction depends upon the weight of the load, the nature of the roads, state of the weather, and whether the roads be hilly or level. There is no more variable factor, and one aspect of this is well illustrated in the following table, which shows the effort required to pull 1 ton over roads of different natures, the surface in all cases being level:

	Force of Traction per Ton.
Smooth surface	31 lbs.
Paved	45 ,,
Macadam	44 to 67 lbs.
Gravel	150 lbs.
On arable land	200 ,,

In practice, the force of traction on a level macadamised road is regarded as equal to one-thirtieth of the load.

There are other features, apart from the nature of the road, which influence the question of effort in draught—for instance, the height of the wheels, the width of the tyre, the presence or absence of springs. These points are only referred to; they belong to the realm of mechanics, but their physiological bearing in increasing or reducing the effort required is well known. Experience goes to show that eight hours' work, at a walking pace of three miles per hour, with a load drawn without difficulty though with effort, constitutes a working day. If the load or pace be increased, the period of labour must be reduced.

The amount of work performed is spoken of as *foot-tons* or *kilogrammeters*—viz., so many tons raised 1 foot or so many kilogrammes raised 1 meter (p. 438). The published tables of work by Redtenbacher, Rankine, Morin, etc., are all too high. These place the normal daily work of a horse at from 6,200 to 6,700 foot-tons (1,926,544 to 2,071,104 kilogrammeters). Kellner and Wolff, in their experiments on nutrition in horses, caused 2,154,000 kilogrammeters of work (7,000 foot-tons) to be performed daily on a circular dynamometer,* but the writer believes that the following more closely approximates to what should be demanded for regular daily work:

A moderate day's work = 3,000 foot-tons.
A hard day's work = 4,000 foot-tons.
A severe day's work = 5,000 foot-tons.

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* This is the amount Watt's horse would have performed in eight hours.

As a means of conveying to the mind the value of quantities which cannot be visualised, the following table has been compiled; the work is equivalent to 3,000 foot-tons, it being assumed that the weight of the animal, together with the weight carried, is equal to 1,000 pounds:

Walking at	3	miles per	hour for	8·7	hours.
,,	4	,,	,,	5·3	,,
,,	5	,,	,,	3·7	,,
Trotting	8	,,	,,	1·5	,,
Cantering	11	,,	,,	1·0	,,

It must not be forgotten that in addition to the effort required to carry or drag a load there is another source of expenditure—*i.e.*, the force required to move the animal's own body weight through space. Many observations have been made to ascertain what this amounts to, but no definite statement can be made, as the question of velocity comes in. It takes more to move the body at a fast than at a slow pace. At the average walk the effort amounts to about one-twentieth of the animal's body weight for every foot of ground passed over—say an effort of 50 pounds; it has, however, been placed much lower.

It is a very difficult matter to obtain exact information regarding the work performed by horses. Fortunately, a good deal of precise information was collected many years ago in connection with the wear and tear of animals, at a time when road-building in this country was being scientifically studied, and still later when the running of coaches had, in consequence of the improvements in the roads and the general improvement in the care and management of horses, become an art of national importance. Information was thus obtained on the force of traction over different gradients, and the amount of work expected from the horses. The following table is by Stewart;* it shows the daily distance travelled, the velocities, the weight of the load, and number of working hours in Scotland:

CARRIERS (TWO WHEELS).

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Hours Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
2¾	22	26	13	8	6	132
3	27	34	17	9	4	108

In the last observation it will be observed that the increase in pace, in distance travelled, and in load, leads to a reduction in the number of working days.

WAGGONS (FOUR WHEELS).

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Hours Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
2	22	60	30	11	6	132
4	22	40	20	5½	6	132

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* 'Stable Economy, 1840.

In the second table the pace is increased, the load reduced, and the working hours diminished by half.

STAGE-COACH.

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Hours Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
8	16	32	16	2	5	80
9	16	46	11·5	1¾	3	48

MAIL-COACH.

Velocity in Miles per Hour.	Daily Distance in Miles.	Gross Weight of Load.	Weight pulled per Horse.	Number of Working Minutes Daily.	Number of Working Days Weekly.	Mileage Weekly.
		Cwt.	Cwt.			
9½	9	35	8·7	57	7	63
10	8½	30	7·5	51	7	59½
11	8	30	7·5	44	7	56

In the above table a small increase in pace necessitates a reduction in the load and distance travelled, and in the duration of the period of work.

The draught employed in the stage-coach in the example given was 62½ pounds per horse on the level, which in the mail-coach was reduced to 40 pounds per horse. It is manifest that with an increase in velocity something must yield—either the effort must be reduced or the duration of labour, or both. It has been shown by actual experiment what amounts of increased effort are required to pull a definite weight (1 ton) on a good road at varying velocities and on different gradients.* In the following table only one gradient, a very easy one, is taken for the purpose of illustration:

	Four Miles an Hour.	Six Miles an Hour.	Eight Miles an Hour.	Ten Miles an Hour.
	Lbs.	Lbs.	Lbs.	Lbs.
Level	76	80	85	91
1 in 64	109	115	120	126

This shows the increase in force required, even on a good road, for every increase of velocity, and the extra effort needed where a load has not only to be drawn, but lifted through a height, as it has to be in the case of uphill work.

The Physiology of Draught.—The horse, with its horizontal spine, was never intended to carry weight; its muscular power is best exerted in hauling, owing to the size of the base on which the animal stands and the immense weight which can be thrown forward beyond the base. The horse in draught allows his weight to act as a falling body, but it would be of no mechanical value if it fell vertically; it has to fall obliquely, and to secure this the feet are employed as a means of purchase, while the body is kept on the move.

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* 'A Treatise on Roads,' Parnell, 1838.

In ordinary draught-work simple pressure against the collar suffices to move the load, but where the latter is considerable the animal gets closer to the ground, bending both knees and hocks in order to obtain a foothold, and pressing forward from the hind-feet especially on starting. In starting a heavy load the diaphragm is fixed, the abdominal muscles tense, those of the hind-quarters so shortened that the skin over them is thrown into ridges; the muscle tensing the fascia of the thigh stands out like a cord, and if the animal is ascending a hill, the toes of the fore-feet are turned in, perhaps in order to increase the size of the chest by turning out the elbows. In heavy draught body weight tells, and in well-made horses body weight and height go together. The increase in body weight for increase in height may generally be considered to be 1 hundredweight for every 4 inches (1 hand); so of two horses, one of 15 and the other of 16 hands, all other things being equal, the latter should be able to exert a force in draught roughly 112 pounds greater than the former. Neither height nor weight govern the indefinable quality of spirit and determination. Of two horses of equal weight and similar build, one may be invaluable, the other worthless, as a worker (see footnote, p. 438).

The strain in heavy draught is not confined to the limbs; it is impossible for a horse to start a weight unless the muscles of the back and loins are fit, and it is equally impossible for him to stop it unless these parts are in sound working order. In heavy draught-work on the level it may sometimes be noticed that the toes of the fore-feet are the first to make contact with the ground. This is due to the animal's being unable to extend his shoulders properly owing to the load. Though the horse is designed to drag weight, he drags it well only on a level. Uphill his power rapidly diminishes, owing to the effort required to *lift* both the load and his own body weight as well as to drag them (p. 440). If, for example, he hauls 1 ton on the level with an expenditure of 60 pounds, he will require to exert a force of 223 pounds to ascend a hill of 1 in 14, and this second rate of effort is made up of 156 pounds to counteract the gravity of the load, and 67 pounds that of his own body weight. So badly, indeed, does a horse climb a hill with a load, that Desaguliers* stated that, if the hill be steep, three men, each carrying 100 pounds, will ascend it faster than a horse dragging 300 pounds. A horse drawing a load on a good hard road with a rise of, say, 1 in 20, is really lifting one-twentieth of the load, besides overcoming the resistance.

A perfectly level road is not the most favourable for work; this was proved to be the case during the old coaching days. Mail-coach contractors found that horses lasted longer on roads with gentle undulations, and this was rightly explained as due to fresh muscles being brought into play and others eased off (see p. 441). The most favourable gradient is 1 in 40, or an angle of a little over 1 degree. This is also the steepest declivity down which a vehicle will not roll of its own weight, and is known as the *angle of repose*. The steepest hill down which a horse can be driven at a fast trot without danger is a smooth road of 1 in 35, equal to 150 feet in a mile, or an angle of about 1·5 degrees. A road of 1 in 25, a little over 2 degrees, is an easy hill to climb; one of 1 in 20, nearly 3 degrees, takes three times as much effort as on a level. A rise of 1 in 15, nearly 4 degrees, is steep, and 1 in 12, rather more than 4·5 degrees, is a severe hill. The question of severity depends upon the length of the hill and weight of the load; one of 1 in 9, a little over 6 degrees, may be ascended by a single horse with a light load. A hill of 16 degrees, nearly 1 in 3, is impossible for any form of draught or for anything but a *led* riding-horse; it is a dangerous hill for a man to descend mounted.

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* 'A Course of Experimental Philosophy,' 1763.

In the descent of a hill the force of gravity acts with, instead of against the horse, but where the inclination is so steep that a marked effort has to be made to hold back the body and load, no benefit is obtained; for example, a gradient of between 5 and 6 degrees requires as much effort to descend as work on a level.

Strength of Horses.—A comparison between the strength of a horse and that of a man has frequently been made, and the amount of a horse's strength variously stated at the strength of from five to seven men. We have found that most horses weighing about ½ ton will just pull seven men along, but in the case of a notoriously powerful draught-horse weighing 14 hundredweight, his strength was equal to thirteen men, whom he dragged very slowly along. This, however, is most exceptional. The greatest force a horse can exert for a few seconds in a steady pull is known as the limit of his strength; no horse can possibly exert in draught a force equal to that of his own body weight. The writer tested the question on the dynamometer, and found that horses pulled, according to their spirit, from 65 to 78 per cent. of the body weight.* The grouping obtained was as follows:

Excellent pullers,	78·5	per cent.	of their	body weight.
Good ,,	77·6	..	,,	,,
Fair ,,	70·6	,,	,,	,,
Bad ,,	65·6	,,	,,	,,

The only horse he met with which pulled 88 per cent. of his own body weight was the animal mentioned above as moving thirteen men.

The **Weight a Horse should Draw** is a question frequently asked. Other things being equal, an animal's power of traction varies directly as his body weight. An attempt has been made by the writer, working on these lines, to ascertain, in the regular draught-work performed generally throughout the country, what proportion the total load bears to the horse's body weight. In this way it is hoped data have been obtained which will enable the question of overloading to be dealt with on a sound basis.

The mean of 650 observations in England was that the horse dragged a load equivalent to 2·53 times his body weight. From the nature of the inquiry it was impossible to avoid favourable cases being selected, but subsequent investigations, where this was specially avoided, show that for work outside towns and cities this ratio may be accepted. In cities, where the roads are good and friction reduced to a minimum, the ratio of load to body weight may be raised to 1 to 3·5. In Lancashire the mean ratio is 1 to 3·5, but in individual cases it may be much higher, even 1 to 5·5. These represent heavy loads pulled short distances by specially heavy horses and for a small number of hours only, whereas the ratio of 3·5 is for eight working hours a day on good roads, though moderately hilly.

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* 'The Maximum Muscular Effort of the Horse,' *Journal of Physiology*, vol. xix., 1896.

Eighty years ago Stewart put the load for slow draught at 22 to 30 hundredweight, cart included. A large contractor at Manchester, in his evidence before the Strathnairn Committee fifty years ago, stated that nothing beyond 25 hundredweight for ordinary draught-work (exclusive of the cart) should be placed behind any horse, no matter whether the roads be good or bad. This is in the ratio of 1 to 3·4, and supports the correctness of this proportion. For light draught a load of 15 hundredweight, and for heavy draught one of from 20 to 25 hundredweight, in both cases exclusive of the vehicle, appear to be average amounts. The vehicles are heavy: one of two wheels weighs from 7 to 11 hundredweight, while a four-wheel waggon weighs about 15 to 16 hundredweight.

The following tables present a physiological statement of the question of draught for an ordinary working day of eight hours:

ROADS OUTSIDE CITIES AND TOWNS.

		Ratio of Body Weight to Load.
Walking pace		1 to 2·5
Trotting	two wheels	1 to 2·0
	four wheels	1 to 2·3

ROADS IN CITIES AND TOWNS.

		Ratio of Body Weight to Load.
Walking pace		1 to 3·5
Trotting	two wheels	1 to 2·2
	four wheels	1 to 2·5

For loads in excess of the above, the hours of labour must be reduced, and horses of sufficient substance employed:

				Minimum Body Weight of Horse.
Where the ratio exceeds	3·5,	but does not exceed	4·0,	15 cwt. 0 qrs.
,, ,, ,,	4·0	,, ,,	4·5,	16 ,, 0 ,,
,, ,, ,,	4·5	,, ,,	5·0,	16 ,, 2 ,,
,, ,, ,,	5·0	,, ,,	5·5,	17 ,, 2 ,,

For as long as observations on draught have been made, the fact has been noted that two horses working side by side do not pull the sum of their individual efforts. Three horses working abreast give almost the same power as four horses working in pairs. This has been attributed to such causes as not working in exact rhythm, and, if in teams, to loss arising from being too far from their work. These are the chief sources of loss, but there is another, not, perhaps, so obvious. Horses are very human in some of their failings, and one is an inclination in double harness or in team not to take their full share. The question cannot be further considered here, but carriers and contractors have a special scale of work for pairs and teams, which is less than what each individual horse is capable of drawing.

The following table shows the actual loads drawn in the past by horses in the streets of London. The load includes the weight of the vehicle. The authority is Gordon.[*]

Brewers' team, each horse draws $2\frac{3}{4}$ tons.
Heavy railway van, each horse draws $3\frac{1}{4}$ tons.
Tramway, each horse drew $2\frac{3}{4}$ tons for a distance of 13 miles.
Omnibus, each horse drew $1\frac{1}{2}$ tons for a distance of 12 miles.
Water-cart horse draws 4 tons.
Coal-waggon, each horse draws 3 tons.
Vestry-cart horse draws $2\frac{1}{2}$ tons.

Weight a Horse should Carry.—This question is one especially affecting the vital interests of mounted troops; there is a great difference between the total weight and the *effective* weight an animal can carry. As in the case of draught, the question of weight is largely influenced by that of pace. Generally speaking, the weight an animal can carry bears some proportion to its own body weight, but this rule appears not to apply to the diminutive breeds of horses. The Burmese pony carries a soldier in campaign kit whose feet are within a few inches of the ground. A Korean pony does his thirty miles a day in a roadless hilly country, carrying 160 to 200 pounds. It was stated in 1807[†] that a Shetland pony would carry a 12-stone man forty miles in one day with ease. Lawrence, in 1810,[‡] stated there was a country postman, working between Glasgow and Edinburgh, and riding 16 stone, who carried his 'northern pony' in his arms to avoid paying toll. The South African farmer, standing over 6 feet in height, rides a lightly-built pony remarkable distances, either at a canter or walk. Our own Exmoor and Dartmoor ponies afford similar instances of endurance. Facts somewhat similar to these suggest that as the horse became bigger his spine became less fit to carry weight. At no time is a horizontal spine a weight-bearer. In proportion to his weight a man can carry far more than an ordinary horse, for the reason that he carries it on a vertical spine. The weight carried by pack-horses, at the time when these furnished the only means of communication in this island, was from 16 to 19 stones (102 to 121 kilogrammes) at their own pace. Desaguliers[§] said that in his day (1763) the pack-horses used by the fellmonger and skinner carried heavier weights than any others, and were sometimes loaded with 32 to 40 stones (204 to 254 kilogrammes), carried at a very slow pace. If what we are told respecting the weight-carrying power of the Cleveland pack-horse can be believed, their capabilities exceeded those of any other breed. Culley[||] (1794) is responsible for the statement that three Cleveland mares each carried 50 stones (318 kilogrammes) sixty miles in twenty-four hours, and did it four times a week. Youatt[¶] states that mill-horses have carried 65 stones (413·6 kilogrammes) two or three miles. One would hesitate to accept the correctness of these loads, were it not that extraordinary weights may be carried by perfectly trained men. A Kashmir coolie will carry 3 hundredweight on his back up a steep hill, while the limit of strength of a Turkish or Egyptian porter does not appear to be reached either by a ship's boat or a large office safe, carried on the back and supported by a band around the forehead. An ordinary man will carry for long distances a third of his body weight, and for short distances more than his body weight. The writer has shown that the effective weight a horse in good condition will carry for long distances lies between one-sixth to one-fifth of the animal's own body weight.* The mean weight of a cavalry horse is 1,100 pounds (500 kilogrammes), so that the *effective* weight he is capable of carrying may be taken at 14 stones (83·2 kilogrammes). Cavalry horses are called upon to carry as much as 20 stones, or 280 pounds (127·2 kilogrammes), roughly, one-quarter of the body weight, an amount greatly in excess of their strength.

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[*] 'The Horse World of London,' W. J. Gordon, 1893.
[†] 'The Complete Farmer.'
[‡] 'Treatise on Horses.'
[§] *Op. cit.*
[||] 'Observations on Live Stock.'
[¶] 'The Horse.'

Apart from the features touched on above, the main physiological fact connected with weight-carrying in horses is that the muscles of the back and loins must be conditioned for the work. An animal in the hardest condition for draught purposes is quite unfit to carry a man; the muscles of the back and those beneath the loins are unable to carry weight unless the animal is properly conditioned beforehand. And this holds good for any class of work which necessitates the employment of a fresh and unskilled group of muscles.

The Speed of Horses—*The Gallop.*—The fastest pace at which a horse has been known to gallop is at the rate of 37·69 miles an hour. The animal was Salvator, who in 1890 was galloped on a straight course against time. Flying Childers, the fastest horse known in this country, galloped 3¾ miles at a velocity of 34¼ miles an hour. In another trial of over 4 miles the speed attained was an average of 33·62 miles per hour. Flying Childers has been credited with galloping a mile in a minute, but this is impossible. The mean velocity for the Derby during a period of ten years was 33·54 miles per hour, the distance being 1½ miles. For the Lincolnshire Handicap, the distance of which is a mile, the average speed for ten years was 33·84 miles per hour. The ordinary gallop varies from 12 to 14 miles an hour. The length of the stride is from 15 to 19 feet for the average horse, for the race-horse considerably more (see p. 679). Eclipse and Flying Childers were credited with a stride of 25 feet.

The Canter varies greatly in velocity, depending, as we have seen, on the length of the spring. The stride may be from 9½ feet in a slow, to 11½ feet in a fast, canter (see p. 677).

The Trot is generally performed at a pace of 7½ to 8½ miles per hour, the length of the stride being between 7 and 10 feet (see p. 672). When trotting matches were popular in this country, some remarkable feats of endurance were obtained. In 1780† a mare trotted 16 miles in 58½ minutes, carrying 12 stone. She repeated the performance when eighteen years old. In 1785 Archer trotted 16 miles in 54½ minutes, but died the next day. In 1800 Phenomenon trotted 17 miles in 56 minutes, and in the same month repeated the distance in 53 minutes. In America, where trotting has reached a degree of excellence unknown elsewhere, some astonishing velocities have been obtained, the mile being covered in 1 minute 58½ seconds, or 30·4 miles per hour.

The Walk of an ordinary horse is a mile every 15 minutes, the length of the stride being from 5 feet 6 inches to 6 feet (see p. 671).

Endurance Tests.—Some years ago long rides were inaugurated on the Continent with the object, it was stated, of encouraging the development of the horse for long-distance work in war. These rides are practically physiological experiments, and are consequently of interest. The first was from Brussels to Ostend, a distance of 82 miles. The winner covered the distance in seven hours. Of 61 horses entering, 17 died, and 17 got no farther than the sixty-second mile. In subsequent rides the principle of racing was abolished, and the essential factors governing the results were the maintenance of condition and fitness. Two of these rides may be briefly referred to. One year the distance was 250 miles. This was covered in 50 hours, the last 53 miles being completed at 12½ miles an hour. Another year the distance was 93 miles, which was covered in 10½ hours. Out of 47 starters only 24 came in, and but 15 of these were qualified. Tests such as these are no indication of the endurance of the average horse, for in all these trials the animals are the pick of many thousands, and, this notwithstanding, we have seen that 50 per cent. fell out in the last trial above recorded.

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* 'The Weight of a Horse and its Weight-carrying Power,' *Journal of Comparative Pathology and Therapeutics*, vol. xi., No. 4, 1899.

† J. Lawrence, *op. cit.*

Two features in these tests need noting. One of these is expressed in an aphorism as old as horses themselves. It is the physiological truth that 'it is the pace which kills.' The other raises the question of whether there is any deterioration in the stamina of horses. Are they as capable of withstanding fatigue as the horse of, say, two hundred years ago? A good deal of evidence might be brought forward, including that mentioned on p. 690, to show that the same powers of endurance are not exhibited, and the explanation would appear to be that with an increase in body height there is a falling off in stamina. The standard of height in horses generally has been raised in order to obtain greater speed in the case of the race-horse, and in other breeds to meet the demands of fashion. But with this increase in stature there certainly appears to be a reduction in stamina. The cavalry of Frederick the Great astonished Europe, and what they did constitutes an object-lesson for cavalry for all time. But in order to get his results the same class of horse must be employed. The standard of height for cavalry since his day has been raised 4 inches and over.

CHAPTER XVII

THE FOOT

HORNS, nails, claws, and hoofs represent a modified form of epithelium, and the tissues from which these are secreted correspond to the deep layers of the skin. The other horny structures found connected with the skin of the horse—*i.e.*, the chestnuts and ergots—have a similar origin. Considered by itself, a piece of horn, a claw, or nail, would not appear to possess any special physiology; but when the nail surrounds and completely encloses the end of the limb, as it does in the ungulata, a special physiology arises, and this reaches its highest development in the solid-footed horse. The foot in this animal has become a highly specialised structure, for the purposes of resisting wear and tear, of supporting the weight of the body, and of saving the foot and limb from concussion. If it were merely a block of horn on which the horse stood, it would offer nothing of special interest.

A foot consists of three feet, each enclosed within another. Externally there is the hoof or horn-foot; within this is a complete counterpart in fibrous and vascular tissue known as the sensitive foot, and the latter is moulded upon a bony structure which in appearance resembles a miniature foot. It is usual, however, to regard the foot as being divided into two portions, an insensitive and sensitive, or an external and internal, the latter term connoting both the vascular and the bony foot. The internal and external feet are exact counterparts of each other, the former being on a smaller scale, to enable it to fit into the external foot in the same way as a finger fits into a glove.

The external and internal feet are not independent of each other—one is the complement of the other. The external does not produce itself; it is dependent entirely on the internal for every horn cell it possesses. The internal foot cannot tolerate pressure, not even touch; it is dependent on the external foot, for the circumstance that, in spite of its highly sensitive nature, it is throughout the life of the animal enabled to be kept within $\frac{3}{4}$ to $\frac{1}{2}$ inch of the ground without causing pain.

Growth and protection are not the only features in the foot. No one can listen to the thuds of the galloping horse, or the clatter of one trotting, without realising that every time the feet come to the ground there must be considerable concussion unless mechanisms existed for its prevention; and no thoughtful person will have any difficulty in realising that the horse's foot represents a remarkably small pedestal for such a bulky body to be carried upon. These are the essential features to which attention must be directed in the physiology of the horse's foot, and must, from their paramount importance, be considered in detail. In order to elucidate them, it is desirable to glance at some of the structural features of the parts concerned.

Bones of the Foot.—The core of the foot consists of bone, around which all the other structures are moulded. The bone is not one solid piece, such as it might be imagined would be necessary in such a position, but, on the other hand, consists of three pieces. One of these is the pedal bone, which is a miniature foot in shape (Fig. 231), while its substance is porous to such an extent as to resemble pumice-stone in appearance and density. A second bone, the navicular, is very small, of peculiar shape, dense in structure, rests slightly on the pedal bone, and is mainly held in position by ligamentous tissue. The third bone belongs partly to the foot and partly to the limb. One might suppose that the pedal bone should occupy the whole of the interior of the hoof, as high as the coronary edge and as far back as the heels, but this is not so. It only occupies a portion of the internal foot (Fig. 232), mainly situated towards the anterior and lateral parts; the posterior part of the foot contains very little pedal bone, but the deficiency is made up by the introduction of two large plates of cartilage attached to it, over which the structures are reflected and moulded as on the bone itself. This singular deficiency of bone, in a part where one might be led to regard its existence as a necessity, and the presence of large cartilaginous plates to take its place, are due to the lateral movements the foot has to perform, and which could not be carried out if the bone were proportioned relatively to the structure within which it fits. The pedal bone is not placed parallel to the ground, but fits within the hoof, with its toe slightly lower than its heels (see Figs. 219 and 237).

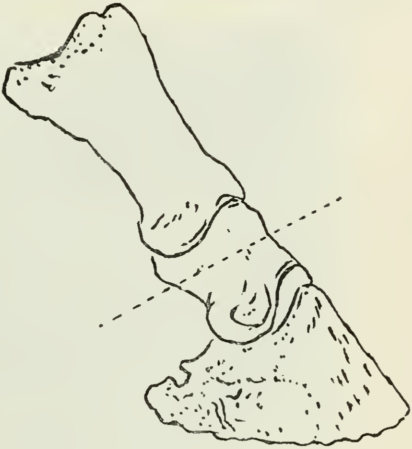

Fig. 231.—Pedal Bone and Corona (Modified from Leisering).

The dotted line through the latter indicates the portion buried within the foot, or hidden by the soft structures at the back.

The Foot-Joint.—Three bones form the foot-joint (Fig. 233). The question naturally arises why the joint is not composed of two bones instead of three, and what advantage is gained by the introduction of a small dense bone, such as the navicular, into the articulation. The articulation furnished by the pedis is much smaller than that provided by the corona, but by the introduction of the navicular, the pedis plus navicular surface is nearly, but not quite, equal to the corona surface. One use of the navicular bone is to increase the articular surface of the pedis. But it is conceivable that this small articular surface of the pedis might have been increased in some other way than by the introduction of a distinct bone and other complicated apparatus, and it is evident that the value of the navicular articulation does not depend entirely on the fact that it increases the size of the joint, but that it supplies what elsewhere has been spoken of as a yielding articulation (see pp. 654 and 656). The use of this yielding articulation is to save direct concussion. During locomotion, when the foot comes to the ground, the weight through the corona falls in the first instance largely on the navicular, which under its influence yields slightly in a downward direction; from the navicular the weight is transferred almost entirely to the pedis, which also yields slightly under its influence, and in this way direct concussion to the joint is prevented.

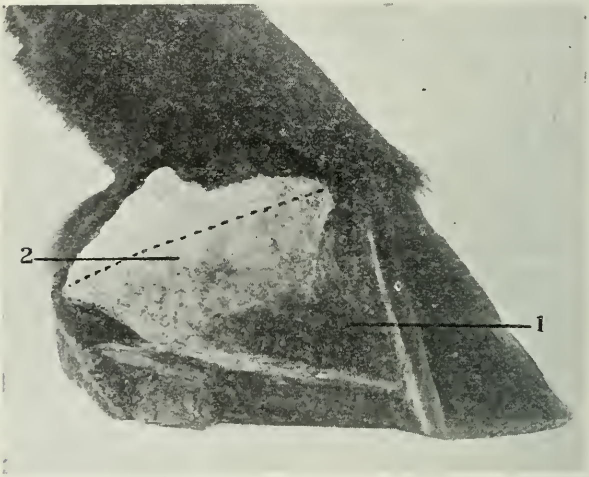

FIG. 232.—THE WALL PARTLY REMOVED IN ORDER TO SHOW THE POSITION OF—(1) THE PEDAL BONE; (2) THE EXTENT OF THE LATERAL CARTILAGE.

The dotted line through the latter indicates the portion within and without the hoof. In the figure the cartilage has curled in and shrunk a little from exposure. It will be noted that the pedal bone is lower in front than behind.

The Navicular Bone and Bursa.—The navicular would be of very little use for the above purpose, if it depended on being kept in position solely by the delicate ligaments which have origin from it. Its chief support is the broad expansion of the perforans tendon which passes beneath it; between the tendon and the bone the most intimate fitting occurs, and a synovial apparatus exists to save friction. It is probable that the perforans tendon and the inferior face of the navicular are more closely adapted to each other than any articulation in the body, excepting some of those found in the knee and hock joints. Briefly, then, the small dense navicular bone is enabled to form a yielding articulation in the foot, owing to the manner in which it is supported in position by the powerful perforans tendon. It might be urged on purely theoretical grounds that a small bone thus placed in the foot would be very liable to damage, and such is clinically true. There is no intention here to touch on the subject of navicular disease, excepting in so far as it helps to elucidate the physiology of the part, but it is permissible to regard the lesions of navicular disease in the light of physiological experiments, and to learn from them how intimately the freedom and elasticity of a horse's action depend upon the navicular bone, and how the stilty, pottering, shuffling gait arises in the animal when this bone is no longer capable of performing its functions properly. The very close support afforded to the navicular by the perforans tendon may possibly be a cause of disease, for the conclusion has been forced on the writer that, under the influence of the weight of the animal, and the counteracting influence of the perforans tendon, the navicular bone must be exposed to considerable compression (see Fig. 233). This compression exists, not only during locomotion, but also during standing. The only complete rest from compression which the navicular bone of the fore-limb obtains is while the animal is lying down. Those of the hind-limbs are relieved from pressure every time the horse rests the leg by flexing the hock, and no case of navicular disease in the hind-feet has ever been known (p. 648).

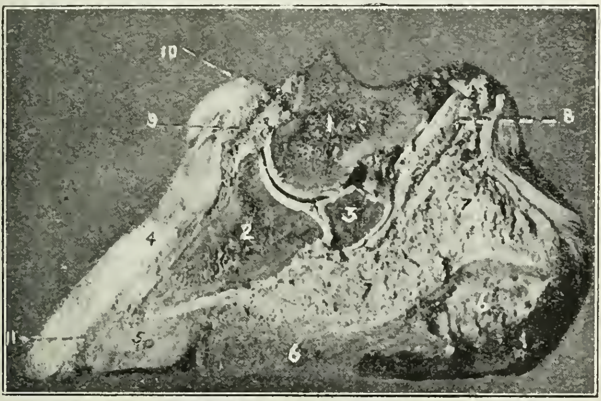

FIG. 233.—LONGITUDINAL SECTION OF THE FOOT.

1, The corona; 2, the pedis; 3, the navicular; 4, the horn wall; 5, the horn sole; 6, 6, the foot-pad; 7, 7, the plantar cushion; 8, the perforans tendon passing under the navicular bone, to be inserted in pedis; 9, the wall-secreting substance; 10, the extensor pedis tendon; 11, junction of wall and sole, the 'white line.'

The navicular bone does not exercise any pulley function in connection with the perforans tendon, such as has been usually described—that is, if by the use of the term ' pulley ' it is intended to convey the impression that some mechanical advantage is obtained. It is true that by passing beneath the navicular bone the direction of the pull of the tendon is altered, but no mechanical advantage is thereby derived. The perforans tendon at its insertion spreads out fan-shaped, and is attached over a considerable semilunar surface of the pedal bone; so extensive is this attachment that it is erroneous to believe the tendon plays over the navicular bone. It is a fact that movement occurs between the tendon and the bone, but the tendon is passive, while the yielding of the navicular bone under the influence of the body weight is the active agent. It is interesting to observe the direction in which the largest amount of friction occurs between these two surfaces. Reasoning from the position of the parts, one would think it occurs at the moment the foot comes to the ground; but if the eroded tendon of navicular disease be examined, it will be observed that the fibres are all stripped *upwards*, and rarely or never downwards. This points to the greatest friction occurring, not when the bone yields under the weight, but when it returns to its place as the body, under the influence of the flexor tendon, passes over the foot. The frequency with which the middle of the ridge of the navicular bone, and the area on either side of it, are affected with disease points to this part as being the seat of the largest amount of pressure.

Lateral Cartilages.—Attached to each side of the heel of the pedal bone is a large curved plate of cartilage, in parts fibrous, in others hyaline in nature. So extensive is this plate that it reaches high above the margin of the hoof—*i.e.*, outside the foot in an upward direction as far forward as the coronet and as far back as the heel (Fig. 232). There is no other structure in the body with which this arrangement can be compared: a bone possessed of two large cartilaginous wings is a something peculiar to the foot. The use of these cartilages is intimately connected with the main principles of the physiology of the foot, to be dealt with later.

Plantar Cushion.—Placed between the two plates of cartilage just spoken of is a large somewhat pyramidal-shaped body known as the plantar cushion (Figs. 233, 7, 7; 234). In appearance it resembles a fibro-fatty mass, is composed of interlacing bands, is pale yellow in colour, almost destitute of bloodvessels, firm to the touch, yet yielding in its nature.

Mettam* has shown that, though the plantar cushion to the naked eye is fibro-fatty, the microscopical characters show it to be mainly tendinous in structure, the fibres being disposed in bundles running in different directions; uniting the bundles is a connective tissue, in the meshes of which fat is found in islets, and not abundantly, as one of the older names of this body implied.† There is only a small amount of elastic tissue present. The position of the plantar cushion in the foot is at the posterior half, between the cartilages, rising up above the level of the hoof and filling in completely the hollow of the heel. Its inferior face is **V**-shaped (Fig. 234), and a complete counterpart of the horn-cushion or foot-pad above which it lies. Its position is shown in section in Fig. 233, 7, 7, and the manner in which it protects the navicular bursa and tendon. The cushion is softer posteriorly than anteriorly, where at its apex it is dense and fibrous. The cushion does not secrete horn, but its surface is covered by a delicate papillated membrane which secretes the horn of the foot-pad.

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* ' The Development and Histology of the Hoof,' etc., by Professor A. E. Mettam, B.Sc., M.R.C.V.S., *Veterinarian*, 1896.

† Nevertheless, W. C. Spooner, of Southampton, writing in 1840 (' Treatise on the Foot and Leg of the Horse '), said analysis showed that the plantar cushion contained no fat in its composition.

Sweat-glands exist in the plantar cushion, situated in and on the side of its central depression. The glands, as figured by Franck, are shown in Fig. 235. A more modern description is given by Mettam. They are large, coiled, single or multiple glands opening on the surface of the horn in the so-called ‘ cleft ’ of the frog by means of tubes, which take very spiral courses. They secrete an unctuous fluid, which helps to maintain the horn in a pliable condition.

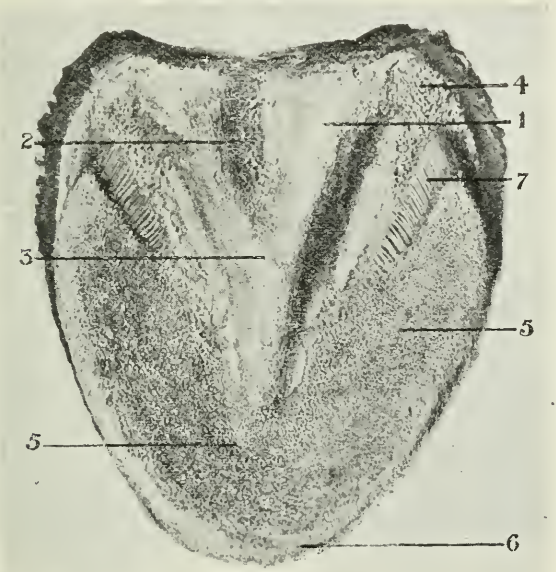

FIG. 234.—THE PLANTAR SURFACE OF THE INTERNAL FOOT.

1, 2, 3, The sensitive foot-pad, or plantar cushion, 1 being the bulbs, 2 the cleft; 4, the termination of the wall-secreting body of the heel, where it blends with the plantar cushion; the numerous papillæ on its surface can be seen; 5, the vascular or sensitive sole, covered by papillæ; 6, terminal ends of the sensitive laminæ, which may be seen around the entire rim; it is at this point where each lamina terminates in four or five papillæ; 7, the laminæ of the wall inflected at the heel, and here forming the sensitive ‘ bars.’

The **Corium** of the foot completely covers the whole of the pedal bone, plantar cushion, and a large surface of the lateral cartilages. This tissue has received various names—viz., from its colour, the vascular foot; from its appearance, the fleshy; from its character, the velvety foot; whilst from one of its functions it has been termed the horn-secreting foot.

The **Vascular Wall** or **Laminal Tissue** (Figs. 236, 4; 237, 6) is composed of corium arranged in the form of a number of leaves lying side by side, which run from the coronet downwards and forwards to the edge of the wall. In number there are about 500 or 600; they invest the entire wall of the pedal bone and the greater part of the lateral cartilages, their extreme vascularity giving the appearance of a thin layer of muscle. The leaves at the toe are longer than those at the heel, where they are very short and turned in under the foot, running forwards beneath it to form the part known as the sensitive bars (Fig. 234, 7).

If a single leaf, say at the toe, be removed and examined, it is

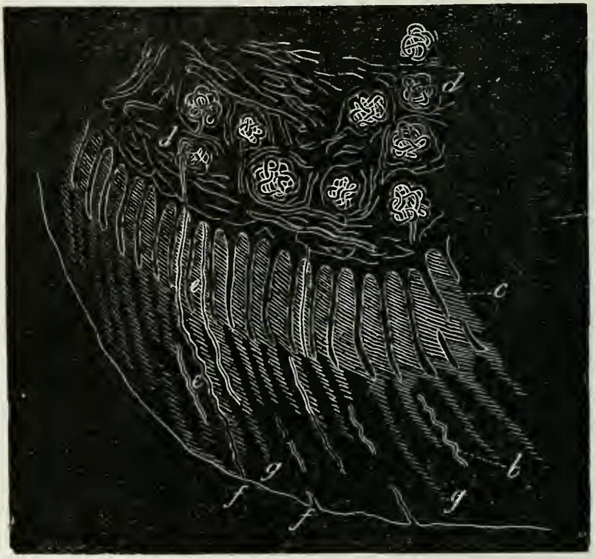

FIG. 235.—THE SWEAT GLANDS OF THE PLANTAR CUSHION (FRANCK).

d, *d*, The glands, the corkscrew-like ducts of which (*e*, *e*, *b*) pass out through the horn of the foot-pad, opening at *f*, *f*, on to the surface of the foot at the cleft. At *c* is the deep-seated portion of the horn of the foot-pad, where it grows from the papillæ of the corium of the plantar cushion; *g*, *g*, are horn fibres seen in longitudinal section.

found to commence immediately under the thick cornice-like structure known as the coronary or wall-secreting body, and to be most firmly attached to the pedal bone; in fact, so intimate is the attachment that it is almost impossible to remove this tissue cleanly from the bone. The leaves under the coronet are very short from front to rear (depth), but as they proceed from the coronet towards the ground they rapidly increase in depth, and attain their full depth about $\frac{1}{4}$ inch or so from their origin. The edge of the leaf is not regular, but denticulated, and at its inferior part each leaf terminates in five or six papillæ. The leaf is extremely vascular—in fact, quite scarlet in colour—the effect over the whole mass of leaves being very striking. If the tissue be examined microscopically, it is found that part of its substance is devoted to leaf-formation, whilst the remainder is a sublaminal tissue, the function of which is to secure the laminæ firmly to the wall of the pedal bone. This sublaminal tissue has been described by Moeller* as consisting of two layers; the one nearest the bone is designated the *stratum periostale*, and acts as the periosteum of the bone (Fig. 238, *b*). Outside this is a layer of fibrous connective tissue and elastic fibres, arranged in bundles, crossing and forming networks; this layer is extremely vascular, and has been designated the *stratum vasculosum*. External to this layer are the laminæ, formed of elastic and connective-tissue fibres, as in the previous layer, only the network is much finer. The laminæ contain numerous bloodvessels and nerves.

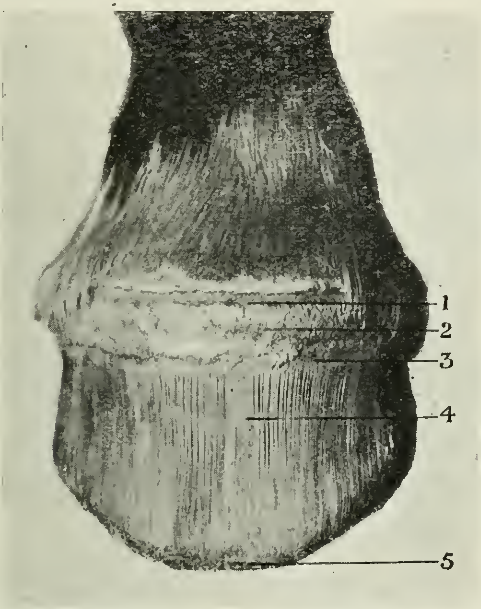

FIG. 236.—THE HOOF REMOVED, AND THE VASCULAR WALL SEEN FROM THE FRONT.

1, Groove between the skin and wall-secreting body from which the *periople* grows; 2, the wall-secreting body; the rough surface is due to papillæ and small adherent fragments of horn; 3, the beginning of the sensitive laminæ; 4, the laminæ; 5, their papillated ends.

The microscopical appearance of a horizontal section of the vascular laminæ is shown in Fig. 238, *d*, from Moeller. Each sensitive lamina is not smooth, as its naked-eye appearance indicates, but denticulated, each tooth-like depression representing secondary laminæ, or laminellæ (Fig. 238, *e*), first fully described by Fleming.† The number of these in a lamina depends on the depth of the primary lamina, but they may be from 60 to 120 in number. It is quite common to find some of the secondary laminæ bifurcate. The appearance presented on horizontal section is very characteristic, and has been aptly likened by Chauveau to a feather, the barb of which is represented by a lamina and the barbules by the secondary laminæ (see Fig. 238). The function of the secondary laminæ has been a fruitful source of discussion.

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* *Veterinary Journal*, vol. v., 1877, p. 114.

† In 1840 W. C. Spooner, *op. cit.*, wrote: 'The inner edges of the laminæ appear fimbriated, like the edge of a fine-tooth comb.'

The Origin of the Horn Laminæ.—No one doubts that the wall grows from the coronet, but great controversy has taken place over the origin of the horn laminæ, some saying they grow like the wall from a part of the coronary cushion, and others affirming that they obtain their origin from the sensitive laminæ. If we were to judge solely by the result of pathological processes, we should say the sensitive secreted the horn laminæ; but Moeller* points out that the sensitive and insensitive laminæ are never in actual contact, and that between them are placed the secondary laminæ of both varieties (Fig. 239). Therefore he argues that the vascular cannot secrete the horn laminæ, but that the secondary vascular secrete the secondary horn laminæ. If a portion of wall be removed experimentally and the vascular laminæ exposed, in the course of a short time the part becomes covered with a layer of horn, with laminæ on its inner surface, and this has been used as a strong argument in favour of the secretion of horn laminæ from sensitive laminæ; but the horn which is thus secreted is derived from the secondary vascular laminæ, and no one contends that these secrete the primary horn laminæ. The following explanation appears to be the correct one: The horn laminæ are secreted from the lower edge of the coronary body; here protoplasmic cells are poured out between the papillæ; these cells are

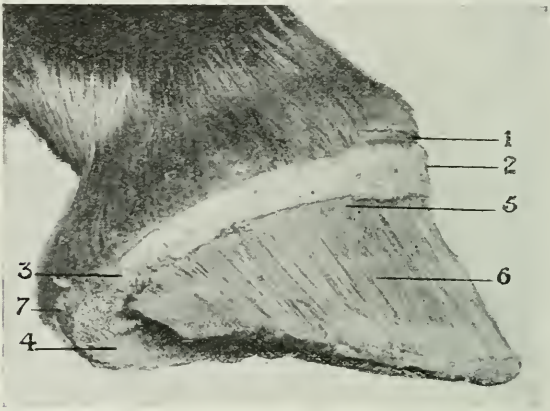

FIG. 237.—THE HOOF REMOVED, AND THE VASCULAR WALL SEEN FROM THE SIDE.

1, The periople groove; 2 and 3, the wall-secreting body; 4, the bulb of the plantar cushion, richly covered with papillæ, and running into 3, with which it joins; 5 and 6, the sensitive laminæ; 7, increase in size of the periople groove at the heels, where a soft horn is formed, which plasters over the junction of the various foot tissues which here meet. Note that the plantar cushion is below the level of the heel of the pedal bone and lateral cartilage.

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* *Op. cit.*

carried down with the wall, being pressed into and moulded between the sensitive leaves, thus becoming horn laminæ, the exact counterpart in shape of the mould in which they are made. All this occurs in the region marked 3, Fig. 236. As the wall grows down the horn-leaves are carried with it, so that there is a perpetual movement occurring between the slowly travelling insensitive and the fixed vascular laminæ. The rate of this movement is probably about 0·0125 inch in twenty-four hours, on the assumption that the wall grows $\frac{3}{8}$ inch in the month. During the time the horny are gliding between the sensitive leaves, the vascular lamellæ furnish them with horny lamellæ; when the wall reaches the sole, the horn lamellæ are left behind, while the primary laminæ emerge with the wall destitute of these structures. This statement does not explain away all the difficulties which could be raised, but suffices for practical purposes.

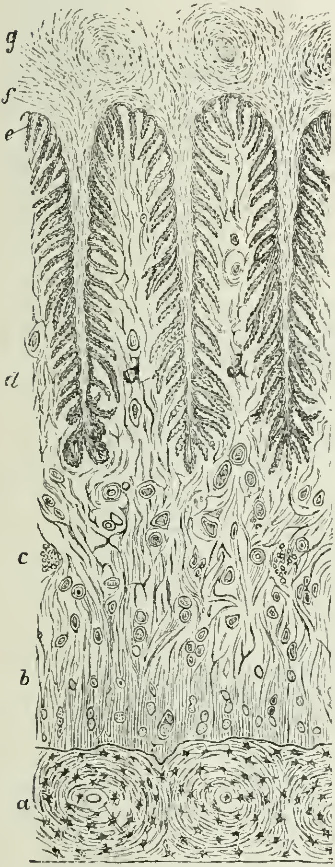

Fig. 238.—Horizontal Section of the Hoof and Vascular Tissues at the Anterior Part of the Horse's Foot (Moeller).

a, Bony tissue of the os pedis; *b*, stratum periostale; *c*, stratum vasculosum; *d*, sensitive laminæ; *e*, secondary laminæ, or lamellæ; *f*, primary horn laminæ; *g*, wall of the hoof, with its horn fibres.

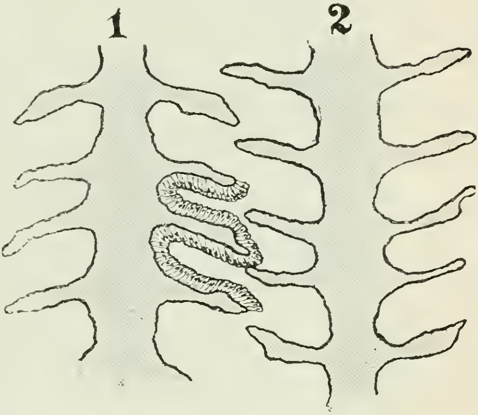

Fig. 239.—Horizontal Section of Portion of a Pair of Laminæ: (1) Sensitive, (2) Horny, Each with their Lamellæ.

The laminæ and lamellæ have been pulled apart; the protoplasmic cells which separate the lamellæ of each type are partly represented. The figure shows that these cells come between both primary and secondary laminæ of each series, which are therefore never in actual contact. It is from these protoplasmic cells that the horn lamellæ are secreted.

The **Wall-secreting** or **Coronary Body** is a thick, half-round, cornice-shaped welt of material situated above the laminæ (Figs. 236, 2; 237, 2, 3); it has received several names, the most rational being that based on its function as the structure which secretes the hoof wall. Externally this body is covered by a highly vascular membrane possessing long papillæ, which are readily seen by immersing the foot in water, while on section it is found to be fibro-fatty in appearance, and consists of a coarse network of elastic and fibrous tissue. It is this latter which forms the main substance of the welt, which projects like a big rim from the sensitive foot. The basement substance takes no part in the secretion of horn; the papillated membrane which covers it alone carries out this function, while the use of the welt is to provide the secreting membrane with a sufficiently firm and extensive surface. The wall-secreting substance extends all round the coronet from heel to heel, where it joins the plantar cushion (Fig. 234, 4). On its superior margin is a narrow groove (Fig. 236, 1), which is the dividing-line between skin and hoof, and from which a peculiar horn known as the *periople* is secreted. This horn cements over the junction between hair and hoof (Fig. 241, X). On its lower margin the coronary substance fuses with fibres from the vascular laminæ. The entire body fits into a half-round groove in the wall, and the papillæ on its surface are lodged in canals formed in the horn. Beneath the coronary welt is a well-developed subcutis, which unites it to the tissues covering the corona and lateral cartilages. The vascular papillated membrane covering the coronary substance is frequently irregularly pigmented corresponding to the colour of the horn wall.

The **Vascular Sole** (Fig. 234, 5) is scarlet in colour, and covered by long papillæ which are lodged in the depressions in the horn sole. In each papilla an artery and one or more veins may be found. The corium covering the plantar cushion is similarly arranged, the papillæ being lodged in canals in the foot-pad or horn frog.

The **Blood-Supply** to the foot is exceedingly rich. With the exception of the internal organs, there is no part of the body so vascular, and the horse has more blood in his feet than in his brain. Mention has already been made of the scarlet appearance presented by the laminæ, the vascular sole, and the tissue covering the plantar cushion. The pumice-stone-like character of the pedal bone is for the purpose of affording passage to the innumerable vessels which are passing from the interior of the bone in an outward direction to reach the vascular tissues; in fact, no description or drawing can adequately convey an idea of the appearance of vascularity presented by the foot. The veins are large and numerous (Fig. 240), and are not provided with valves; some pass through the substance of the lateral cartilage, and a large plexus exists both outside and inside the cartilage. The relation of these vessels to the lateral cartilages and the absence of valves are matters which will be considered later.

The **Hoof**, or insensitive foot, is moulded over the sensitive structures in such a way as to cover them completely, and form in horn a perfect counterpart of the sensitive foot. The hoof is composed of a *wall*, with its inflections the *bars*, a *sole*, and a *foot-pad* (frog); each of these must be considered separately.

The **Wall** is that part of the hoof which can be seen when the foot is on the ground; its division into toe, quarters, and heels is for convenience of description, as no natural division exists. On the exterior of the wall, at the meeting of the hair and hoof, is a rim of peculiar non-pigmented horn, previously spoken of as the **periople.** Under natural conditions it is grey in colour, soft to the touch, and it cements the skin to the hoof. Its non-pigmented condition is rendered evident only when the foot has been soaked in water or poulticed; the cells then swell, and a white curdy rim occurs all round the top of the wall (see Fig. 241, X). It is wider at the bulbs of the heel, where it cements over not only the union of skin with foot-pad, but the meeting-place of the wall and foot-pad. The periople provides the wall with an extremely thin covering, resembling a delicate coat of varnish, which is intended to prevent undue evaporation from the horn beneath.

The **Colour** of the horn of the hoof is commonly described as black or white; to be strictly accurate, it is neither. The so-called black horn consists of various tints of slate colour; the white is pale yellow or buff. It is, however, convenient to speak of black and white feet. In dealing with the skin (p. 315), the colour of feet was touched upon, and it was made clear that it depended upon the colour of the hair of the coronet. If this is white, there is no pigment in the skin, and consequently none in the horn; if it is partly black and white, the foot is striped accordingly. If the coronet is of any other colour than white, the feet are dark; but if these colours are mixed with white, the feet are striped. It might be imagined that a grey horse would have white feet, but a grey horse is not a white horse, and a grey with grey legs has dark feet, but a grey with white legs has white feet. The number of white feet among grey horses is very small.* The physiological importance of non-pigmented horn is its weakness, brittleness, and slow growth, as compared with the pigmented variety. A white foot constitutes local albinism (see p. 316).

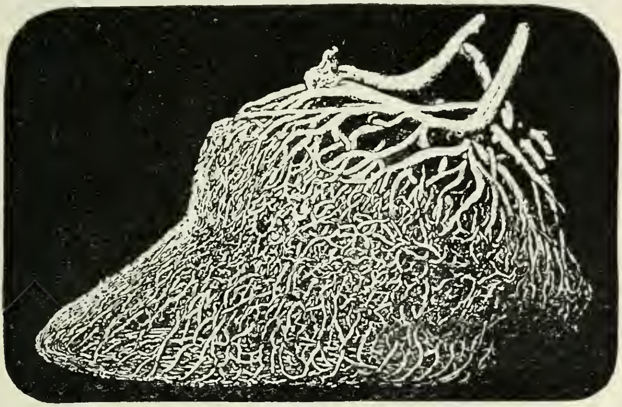

FIG. 240.—THE VENOUS SYSTEM OF THE HORSE'S FOOT (STORCH).

The wall is thickest and longest at the toe, thinnest and shortest at the heel. A gradual decrease in thickness occurs from front to rear (Fig. 242); but if a section of the wall be made in the direction of its fibres, it will be found that whatever the thickness may be at that particular part, it is maintained from the coronet to the ground surface. The greater thickness of the wall at the toe and quarters as compared with that of the heels is connected with the wear and tear of the hoof, and the movements which the latter undergoes under the influence of the body weight. If the wall were as thick at the heels as at the toe it would be a rigid box; it is, however, a yielding box, and the yielding occurs in the region of the thin wall of the heels. The reason why the wall is thick at the toe is that it is here the greatest friction and strain occurs. The wall at the heels is suddenly inflected (Fig. 242, 5), running under the foot in a forward direction for a short distance, and forming an acute angle with the wall. This inflected portion of the wall is called the **Bars** (Fig. 242, 6), and in the gap formed between the two bars is lodged the foot-pad. Thus the wall is an incomplete circle of horn, the circle being broken at the posterior part of the foot, and the piece of wall which might have completed the circle is sharply bent on itself and caused to run in practically the opposite direction. When this arrangement is considered, it is easy to see the advantages gained. The foot is not a rigid body, but a yielding one; and it would be difficult to understand how any lateral movement could take place had the wall been a complete circle. From their position the bars afford additional strength as weight-bearers, for they represent the wall carried within the foot; they also prevent any rupture occurring between the wall and foot-pad during the lateral movements of the foot.

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* I am indebted to the late Captain Martin Millar, A.V.C., for exact information respecting 500 grey horses: 57·3 per cent. had black feet, 34 per cent. parti-coloured feet, and 8·7 per cent. white feet. He also observed that a dark spot on a white coronet frequently colours the hoof out of all proportion to its size.

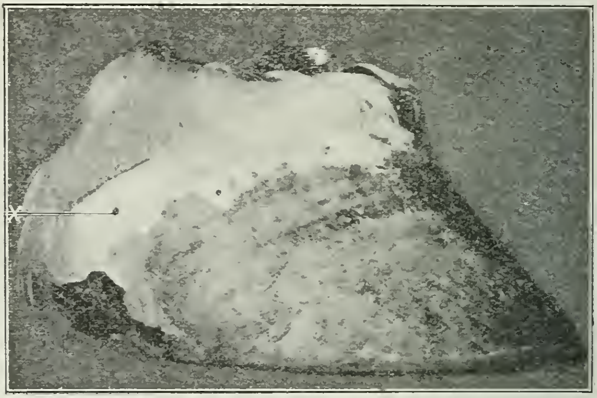


FIG. 241.—THE EXTERNAL FOOT OR HOOF.

The fibrous appearance of the wall may be seen, also the *periople* marked X; the hair of the edge of the coronet is clipped away to show this band of white horn, which for the purpose of the photograph was swollen by immersion in water.

The hind-feet differ from the fore in shape, being more upright and narrower. They do less work, for they are exposed to less concussion, while, from the natural attitude of the horse at rest (p. 648), they are alternately relieved of weight.

On the inside of the hoof-wall a very complex arrangement presents itself. At the upper edge, corresponding to the coronet, is a deep semicircular groove, in which is lodged the thick welt of tissue previously described as the wall-secreting substance. Covering the entire surface of this groove are innumerable pin-point holes, into which the papillæ projecting from the ' substance ' are lodged. The thickness of the wall at any one place corresponds to the size of the coronary substance; the wider it is, the larger the area it affords to the horn-secreting membrane covering it. There are very marked differences in the thickness of the wall. In some horses it is very thick, in others, especially in ' white ' feet, it is extremely thin.

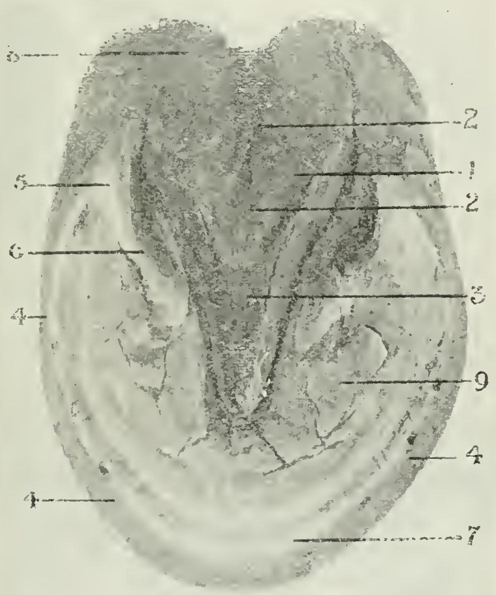


Fig. 242.—The Hoof seen from its Ground Surface.

1, 2, 3, 8, The foot-pad, 2 being the cleft; 4, the wall; 5, its inflection at the heels to form 6, the ' bars '; 7, the white line; 9, the sole. The ' flakes of sole present in an unmutilated foot are seen.

This is one reason why white feet are objected to. Feet possessing a thin wall grow very slowly, and are always a trouble in shoeing; sometimes it is impossible to obtain a fresh hold for the nail without driving the latter high, an objectionable practice which ruins the wall for subsequent shoeing. Slowly growing feet are at once recognised by the numerous nail-holes they contain. The effect of driving a nail into the wall is to cause the horn below the 'clench' to become dry and brittle, owing to the loss of moisture occasioned by the horn tubes being cut across.

Horn Laminæ.—On the inside of the wall of the hoof a number of leaves of horn are found arranged side by side, running all round the foot from heel to heel, and extending from coronet to ground surface. It is easy to see that they correspond in size, direction, and length to the vascular or sensitive laminæ previously described, and, like them, they possess *secondary horn laminæ* or *lamellæ* (Fig. 239, 2). These insensitive and sensitive laminæ fit into each other by the process of dovetailing, which results in extraordinary strength being obtained. So powerful is the union that, in endeavouring to separate them, the vascular laminæ will often tear from the pedal bone rather than rupture the dovetail. In this way the most intimate and perfect union between the vascular and the hoof wall is brought about, and, in addition, other advantages are obtained which will be dealt with shortly. The horn laminæ, as their name implies, are composed of horn, but the secondary laminæ which invest them are composed of cells which are a something between horn and epithelium—*i.e.*, the cells have not undergone a true horny conversion, but remain protoplasmic in nature; this is recognised from the fact that they readily stain with carmine, whereas horn does not. It will be remembered that though the sensitive and insensitive laminæ dovetail yet they are never in actual contact, for between them are the lamellæ, both sensitive and insensitive. The sensitive lamellæ look towards the horn wall, the insensitive lamellæ point in the direction of the pedal bone, so that the dovetailing of the lamellæ is not necessarily effected at right angles to the primary laminæ (Fig. 238). The origin of the horn laminæ has been considered at p. 708.

Horn laminæ are found on the bars, for these, though situated under the foot, are a part of the weight-bearing wall, and possess all its essential structural elements.

The **Sole** of every normal foot is concave inferiorly (Figs. 242, 243), that of the hind-feet being more concave than that of the fore. This concavity agrees with the concavity of the solar surface of the pedal bone, which in itself is ample evidence that the general surface of the sole is not intended to bear weight, though the portion in contact with the wall is a weight-bearing surface (Fig. 244, 6). Soles vary in thickness, some being rigid and firm, others thin and yielding; the sole cannot be too thick. Those shown in Figs. 242, 243, and 244, are excellent specimens of a good sole. The growth of the sole is peculiar; in exactly the same way as was noticed in the wall, the papillæ from the vascular sole fit into pin-point holes in the horn-sole, and horn is developed around them. But here the resemblance ends; while the horn of the wall is capable of growing to almost any length, until, in fact, it curls at the toe like a ram's horn, the horn of the sole can only grow a very short distance before the fibres break off, and scales or flakes of horn are the result; these either fall out or are pulled out. In other words, the foot determines for itself how thick the sole shall be, and, without any assistance, the fibres break off when the proper thickness has been attained, and allow the part to drop out. This shelling out of the sole, which can be seen in Fig 242, is advantageous in the shod foot, inasmuch as the part, not being exposed to friction, cannot wear away. In the unshod foot friction maintains the wall and bars at their proper length (see p. 736, last sentence) so that no natural breaking off of horn fibres occurs.

The union between the vascular and the insensitive sole is brought about by the papillæ on the surface of the former. The extraordinary length and number of these can only be appreciated by examining the parts under water.

The sole and wall are united in a distinctive manner, and the union is indicated by a **white line** (Fig. 242, 7) which runs around the entire junction of sole and wall. The white line represents the layer of the

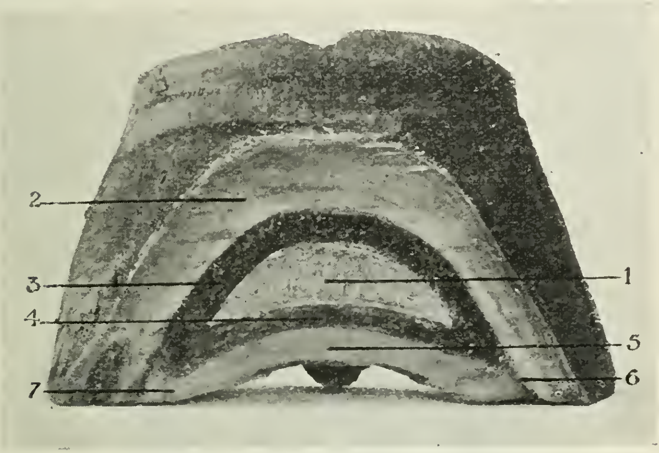


Fig. 243.—A Vertical Section through the Foot, One-Quarter of its Distance from the Toe to the Bulbs of the Heel (Fig. 242, 8).

1, The pedal bone; 2, the horn wall; 3, the sensitive laminæ; 4, the sensitive sole; 5, the horn sole; 6, the junction between wall and sole; 7, the margin of sole capable of bearing weight.

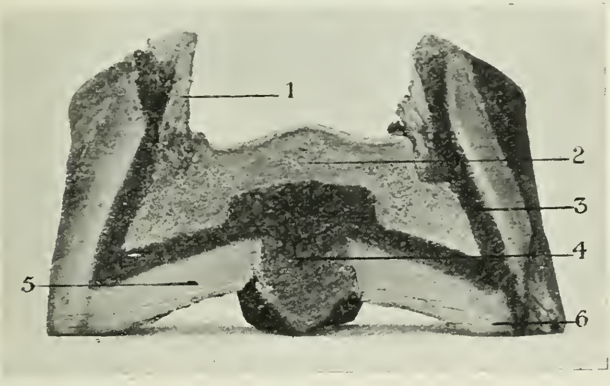


Fig 244.—A Vertical Section through the Foot, One-Half the Distance between the Toe and the Bulbs of the Heel.

1, The lateral cartilage; 2, the pedal bone; 3, the sensitive laminæ; 4, anterior portion of foot-pad; 5, the sole; 6, the weight-bearing portion of the sole.

wall next to the insensitive laminæ (Fig. 245, 6); within this come the ends of the laminæ themselves, and between these and the sole a layer of much softer yellowish plastic horn (Fig. 243, 6). This cement substance is secreted by the four or five papillæ found on the extremity of the sensitive laminæ, shown diagrammatically and microscopically in Fig. 246. The soft cement substance, besides ensuring the union of wall and sole, also admits of slight yielding of the sole, to which reference will be made later. A microscopical examination of the union shows the horn laminæ digitating with the sole; the laminæ are now wavy, and no longer in possession of secondary laminæ (Fig. 246, B). The horn between the laminæ is arranged in concentric layers, being formed by the four or five secreting papillæ on the ends of the sensitive laminæ.

The **Foot-pad,** or 'frog,' as it is vulgarly known, is a pyramidal-shaped piece of horn, accurately moulded over the plantar cushion,

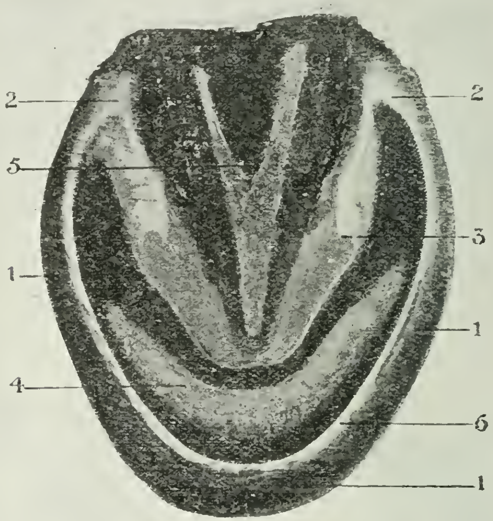


FIG. 245.—HORIZONTAL SECTION ACROSS THE FOOT, ONE INCH ABOVE AND PARALLEL TO THE GROUND.

1, The wall; 2, its inflections at the heels; 3, the bars and convexity of the sole caught in the section; 4, part of the pedal bone; 5, portion of the plantar cushion; 6, the white inner layer of horn between the sensitive laminæ and the outer wall.

and filling up the space left by the inflection of the wall at the posterior part of the foot (Fig. 242, 1, 2, 3, 8). In the foot-pad we meet for the first time a peculiar soft elastic horn, possessing something of the character and appearance of india-rubber. The horn fibres of this structure are wavy, arranged in strata which run at right angles to each other, and confer on the part its fibrous character and elasticity. The horn of the pad contains much more moisture than that of any other part of the foot, and it is the moisture which, aided by the secretion of the sweat glands of the plantar cushion, confers on it its peculiar soft pliable condition. The foot-pad grows from the vascular membrane covering the plantar cushion. The overgrowth of horn is provided against by a method which is a combination of those found in the wall and sole—viz., it is cast off after growing to a certain thickness, while the part next the ground is worn away by friction. In consequence, owing to its rubber-like nature, rags of horn along the edges of the foot-pad are a common and natural condition.

A transverse section of the foot-pad at its posterior part resembles in appearance the letter **W**. The two lower points are the sides of the pad; the space between them is the so-called 'cleft,' or central depression (see Fig. 247, 3). Above the cleft on that side of the pad next to the sensitive foot is a projection of horn known as the '**frog-stay,**' or 'peak.' The function which has been assigned to this peak is to prevent the parts becoming displaced; but its position, shape, and connection suggest that it acts the part of a wedge, being forced upwards under pressure when the foot comes to the ground, and it may thus exert a central pressure on the plantar cushion and assist in the expansion of the foot. But it appears, however, to be more valuable as a means of stimulating the nerve-endings in the plantar cushion, which are especially abundant in this region, and of so acting the part of a touch organ.

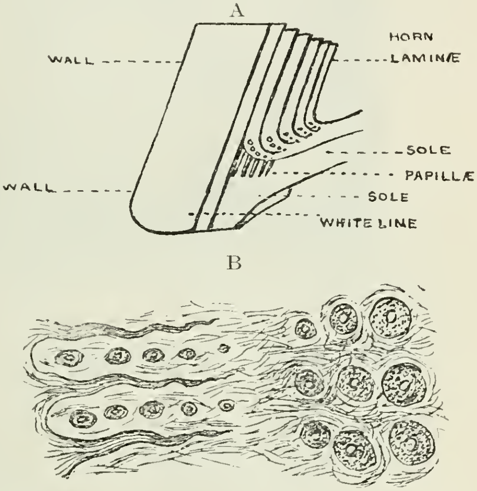


Fig. 246.—The Junction of the Horn Tissues of the Wall and Sole.

A, Diagram of the wall, horn laminæ, and sole, seen vertically. Between each horn lamina may be seen the foramina, into which the papillæ on the terminal end of the vascular laminæ fit. Note the rounded termination of the horn laminæ.
B, Microscopical appearance of a horizontal section of the junction of wall and sole; the horn laminæ are wavy, devoid of secondary laminæ, and between each may be seen the papillæ in section. On the right of the figure the horn tubes of the sole are shown.

The Structure of Horn.—The horn of the foot consists of epithelial cells which have undergone compression and keratinisation, by which latter process they become hard and tough. It is possible to have horn in the foot which is not keratinised, and the two kinds are very readily distinguished by the process of staining. The double stain picro-carmine has a selective affinity for each kind of horny tissue; the carmine picks out the protoplasmic and non-corneous cells and stains them red, whilst the picric acid stains a yellow colour all tissue which has undergone the process of keratinisation. By means of this stain it is easy to determine the character of the horn under examination.

The ultimate horn cell is a very thin, spindle-shaped, oblong, or irregular body (Fig. 248), containing granular matter, a nucleus, and frequently pigment. In all cases the cells are united at their edges and sides by a cement substance. By horn being acted upon by caustic alkalies, the cells are in the first instance rendered clear; they then gradually dissolve, are converted into a gelatinous mass, and finally disappear. The highly alkaline nature of decomposing urine, owing to the presence of free ammonia, being borne in mind, the practical application of this fact in the care and management of the feet is very obvious.

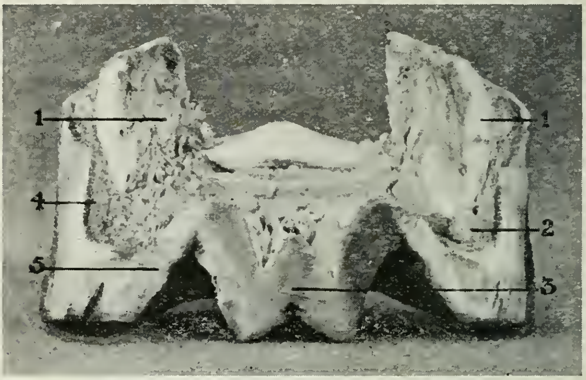


FIG. 247.—VERTICAL SECTION THROUGH THE FOOT AT A POINT TWO-THIRDS THE DISTANCE FROM THE TOE TO THE BULBS OF THE HEEL.

1, The lateral cartilages; 2, heel of the pedal bone; 3, the foot-pad; 4, the sensitive laminæ; 5, the 'bars.'

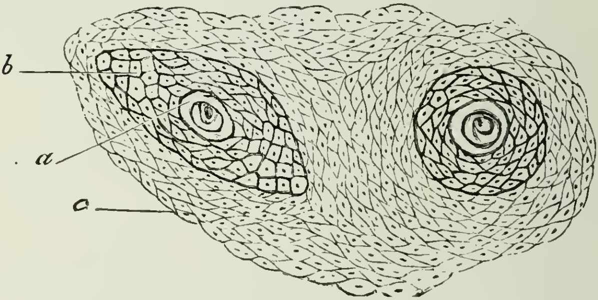
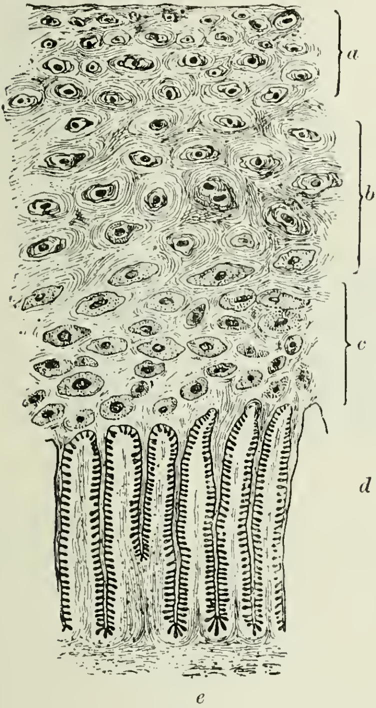


FIG. 248.—HORIZONTAL SECTION OF THE HORN OF THE WALL, HIGHLY MAGNIFIED.

a, Horn tube, a canal containing cellular elements; *b*, the tubular horn—that is, the horn secreted from the papillæ, forming an oval or circular nest of cells around the canal; *c*, the intertubular horn.

If a portion of horn be examined microscopically, it is found that the compressed epithelial structure is tunnelled in such a way as to form canals or tubes, or, at any rate, to form a structure which is tube-like in nature (Fig. 248). These tubes exist wherever the growing surface is invested with papillæ, so that where the papillæ are numerous the tubes are numerous, where they are absent the tubes are absent. The only horny structures not secreted from a papillated surface are the horn laminæ, and consequently in these there are no horn tubes; everywhere else the horn is found to possess a more or less tubular structure. The method of tube formation is simple. The papillæ growing from the various secreting surfaces are lodged in canals in the horn. As the horn grows down from the surface which secretes it, the canal enclosing the papilla gradually slides off, but throughout the length of the horn a tubular appearance indicates where the papilla was at one time lodged, and the cells of these tubes, from their reaction with carmine, prove themselves to be different to true horny structure.



a, *b*, *c*, The outer, middle, and inner portions of the wall, showing the canal system with the tubular and intertubular horn; *d*, the horn laminæ bearing on their sides the lamellæ, shown black: there are sometimes a few short laminæ to be seen—one is shown in the figure; *e*, the sub'aminal tissue, from which the sensitive laminæ may be seen dovetailed between the horn laminæ, and from the sides of which the sensitive lamellæ grow.

FIG. 249.—HORIZONTAL SECTION OF THE HORN AND VASCULAR WALL OF THE HORSE'S FOOT. LOW MAGNIFICATION.

The horn which is secreted in the foot is therefore formed (1) from papillæ found on the secreting surface, and (2) from the spaces between the papillæ. The papillæ form tubular horn, the spaces between them form intertubular horn (Fig. 248, *b* and *c*), and this is arranged in an oval or concentric manner around the canals (Figs. 249 and 250), the cells composing it being so placed that their edges are towards the papillæ. There is, however, a layer of cells which actually forms the wall of the canal, and these are arranged with their sides next it; or, to put it another way, they stand on their edges. In the deep layer of the wall the papillæ produce a much greater secretion, and here the circular or oval masses of cells investing the canal are more prominent; and, further, unlike those in the anterior and middle parts of the wall, they need no reagent to demonstrate their cellular nature (Fig. 249, *c*). If a section of wall be stained with picro-carmine, only the canal contents of the external and middle wall stain with carmine; all the remaining substance takes up the picric acid. In the deep wall this is different; here the whole of the cellular material secreted by the papillæ is stained red, showing that these cells are protoplasmic rather than horny, and partly accounting for the fact that this deep horn is always softer than the middle or external horn of the wall.

If a vertical section of horn be made, the canals are now seen divided in their length (Fig. 250). Though spoken of as canals or tubes, they are really not empty, but throughout their entire length contain cells which are protoplasmic in nature. These, owing to the manner in which they reflect light, give to the part a beaded appearance. The cells contained within the canal are secreted by the apex of the papilla; they do not fill up the entire lumen of the canal.

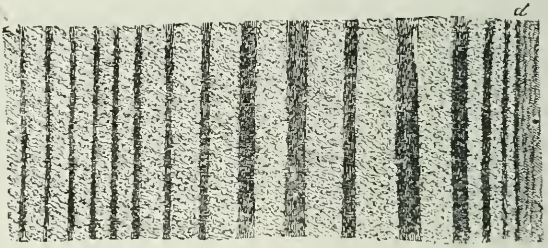


FIG. 250.—MICROSCOPICAL STRUCTURE OF HORN: VERTICAL SECTION OF THE WALL. LOW MAGNIFICATION (AFTER LUNGWITZ).

Note the different size of canals; those on the right are nearest the laminæ; those on the left are towards the outside wall; they are smaller and more numerous than those deeper seated; *d* is a portion of a horn lamina.

The use of the canal system in horn is for the purpose of irrigation; the horn must be supplied with moisture; most of this is obtained through these imperfect canals, the soft protoplasmic canal-wall readily admitting transudation. It is not intended to assert that anything like a fluid is circulating along the tubes, but moisture certainly does find its way down, and is readily imbibed by the surrounding cells. There is no doubt that in the intertubular horn moisture also passes from the secreting surface from cell to cell, and in this way is transmitted throughout the length of the foot. Finally, it can be absorbed from without. Constant evaporation is taking place from the foot, and the loss is made good in the manner indicated. If the invisible moisture which is always escaping from the foot be hindered in its evaporation, the horn becomes sodden, crumbles away, and resembles a grey cheese-like mass. This experiment can be readily performed on the sole and foot-pad by accurately moulding to their surface a sheet of gutta-percha and leaving it there. The practical lesson is obvious: no impervious material should be applied to the foot as a protection, or, if used, it should be ventilated.

Use of the Moisture in Horn.—The amount of moisture contained in horn is something considerable, and the rate at which it evaporates is remarkable.* If parings of the foot-pad be enclosed in a bottle, in a short time the interior will become bedewed with moisture. The use of the moisture is to maintain the elasticity of the foot, and to prevent the part from becoming brittle. The agents whose function it is to prevent the too rapid evaporation of moisture from the wall are the thin, varnish-like layer which covers the hoof, and the natural hardness of the external fibres of the wall. Horn containing but little moisture is in an abnormal condition; it is rigid and brittle; nails driven into the part cause it to crack, and the elasticity, on which the natural shape and usefulness of the foot so largely depends, becomes impaired, or even destroyed. A museum specimen of a foot illustrates these facts very clearly; in its dried condition it is so brittle that, if dropped, it will frequently fracture like a piece of glass; but if such a foot be placed in water for a few days, it comes out as fresh and elastic as though it had just been removed from the body. All that the horn has done is to imbibe water, and the previously brittle substance now becomes yielding and elastic. The entire physiology of the horse's foot is centred around this question of the moisture contained in horn. The presence of moisture confers elasticity, and elasticity of the hoof prevents its fracture under the pounding effects of concussion during work.

Chemistry of Horn.—An analysis of the horn of the foot has given the writer the following results:†

	Wall.	Sole.	Foot-Pad.
Water - - - - -	24·735	37·065	42·54
Organic matter - - -	74·740	62·600	57·27
Salts - - - - -	0·525	0·335	0·19
	100·000	100·000	100·00

The pad contains the largest amount of moisture, and the wall the least. The salts are small in amount, and consist principally of those of sodium, magnesium, iron, and silica, in the form of chlorides, sulphates, and phosphates. Keratin, a substance which replaces the protoplasm originally existing in the cells, is a protein-like body found in hair, nails, and even, in a modified form, in the nervous system; it consists of carbon 51·41, hydrogen 6·96, nitrogen 17·46, oxygen 19·49, and sulphur 4·23, per cent. The sulphur is loosely combined, and it is this, in combination with hydrogen, which causes the offensive odour which arises from diseased feet, sulphuretted hydrogen and mercaptan being formed. Keratin is a very insoluble substance, but is dissolved by strong or by boiling acids and by alkalies. With sulphuric acid it yields leucine and tyrosine, and on incineration gives off the odour peculiar to burnt horn, together with a gas (cyanogen ?) which burns with a peach-coloured flame.

Provisions for Elasticity and Toughness.—From what has previously been said, it can be seen that it is the wall of the foot which supports the horse's weight. On examining the wall, we find it is thickest at the toe, thinner at the quarters, and thinnest at the heels (Fig. 253); it is thickest at the toe owing to the functions performed by this part, leading to excessive wear and tear. As the pad and posterior part of the foot are the first to make contact with the ground (at any rate, in all fast paces), so the toe is the last part to leave it, the final propulsion to the body being given by it, as we have seen in studying locomotion. The object of the wall becoming thin towards the posterior part of the foot is to allow of the elastic movement which has yet to be described. Two physical conditions have to be provided for in the wall—namely, elasticity of the posterior part and toughness of the anterior portion. The first is furnished by the wall being thinner at the heels than elsewhere; but besides being thinner, the wall of the heel contains more moisture than the wall of the toe, and this moisture insures its elasticity. The younger the horn—viz., the nearer to the coronet at which it exists—the more moisture it contains; the farther away from the coronet, the less moisture it possesses, and the tougher and more resisting the horn. Toughness of the anterior part must now be considered.

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* James Clark ('Observations on the Shoeing of Horses') described the moisture in the foot in 1782. He speaks of the insensible perspiration exuding, and states that if a newly-pared piece of frog be held up to the light of the sun, vapour may be seen arising from it.

† 'Chemistry of the Hoof of the Horse,' *Veterinary Journal*, vol. xxv., p. 313, 1887.

The wall grows evenly from the coronet all the way round; if it grows $\frac{1}{2}$ inch in the month at the toe, it grows the same length at the quarters, and the same at the heels. The anterior part of the wall is longer than the posterior, therefore the anterior is tougher than the posterior, for the reason that the horn is much older at the extremity of the toe than it is at the heel, and being farther away from the coronet, it contains less moisture. The wall at the heel is some months younger than that at the toe; it is thinner and contains more moisture, therefore it is more elastic, but not so tough. The age of the wall is an important factor in the wear of the foot. If it takes from nine to twelve months for it to grow from the coronet to the toe, the piece of wall at *f′*, Fig. 251, is, say, twelve months old, whilst that at *a′* is less than six months old. The horn of the quarter is older than the horn of the heel, and the horn of the toe older than that of the quarter. This provision admits in the unshod foot of considerable friction occurring at the toe without producing undue wear, for the part is hard and tough, while the younger and moister horn at the posterior part of the foot allows of elasticity. In this way the ground surface of the foot is provided with the hardest horn where friction is greatest. In theory, no fraction of an inch of the ground surface of the foot, from toe to heel, is of quite the same age.

The toe of the wall appears to grow faster than either the quarters or the heels, but this is more imaginary than real; it is the tendency of the foot to grow *forward* as well as downward which produces the illusion. That the foot grows forward may readily be determined by experiment, for if a cut be made in the wall at the coronet, say an inch or so from the heels, it will in course of time be carried some considerable distance towards the toe; the exact distance can be determined by observing the obliquity of the horn fibres.

How the Weight is carried by the Foot.—It is universally recognised that the weight of the body is supported by the union of the insensitive with the sensitive laminæ. That the enormous weight of the horse's body should be carried upon—or, rather, slung upon—thin delicate strips of sensitive material on the one hand, and correspondingly delicate strips of horn on the other, is perhaps the most remarkable feature in the physiology of the foot. This union is so firm that it is a matter of extreme difficulty to separate the two surfaces, even by mechanical means. In a single foot the weight is carried on 600 or more primary laminæ, assisted by 72,000 or more secondary laminæ. Those laminæ situated at the anterior part of the foot are exposed to more strain than those posteriorly placed, for the reason that, during progression, the final propulsion of the body comes entirely on them; they are also longer, and have no plantar cushion or foot-pad to assist them, as the shorter, posteriorly placed laminæ have. The latter have their strength increased by the direction in which the weight of the body comes upon them. Instead of bearing it on the length of the

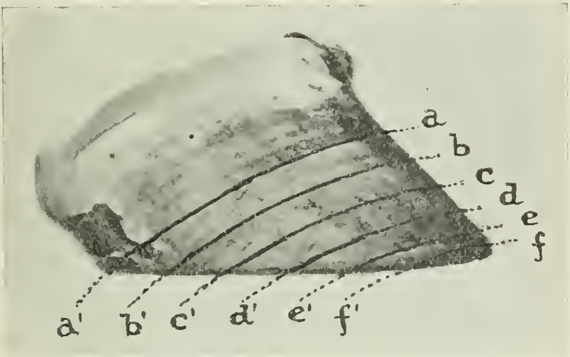

FIG. 251.—DIAGRAM ILLUSTRATING THE AGE OF THE WALL.

a, *b*, *c*, *d*, *e*, *f*, are arcs drawn round the hoof parallel to the coronet; in this way it is ascertained that the age of the wall at *a* is the same as that of the heel at *a'*; the age of the wall at *d* corresponds to the age of the quarter at *d'*. Every portion of the ground surface of the wall is of a different age, being oldest and hardest at *f*, *f'*, and youngest and most elastic at *a*, *a'*.

laminæ, as at the toe, they carry it on the side in such a manner that the work of one lamina at the toe is shared by several at the quarter.

It will be remembered that the laminæ at the anterior and on part of the lateral face of the foot are mainly attached to bone, but on the remaining lateral face and at the posterior part of the foot they are attached to stout cartilage; if a line be drawn through the foot at the junction of these structures (Fig. 252), this feature will be demonstrated; part of the laminal attachment is cartilaginous and part osseous, the cartilaginous portion being situated where elasticity is required—viz., on the posterior face of the wall. The line between hair and hoof shown in the figure indicates that part of the lateral cartilage is within and part outside the hoof. One function of the lateral cartilages of the foot is to afford a movable wall-attachment to the sensitive laminæ, and thereby to enable them to be carried outwards during expansion. A knowledge of the relation of the posterior laminæ to the lateral cartilage explains the cause of lameness in 'side-bone'—viz., the squeezing of the sensitive structures between the wall on the one hand and the ossifying cartilage on the other.

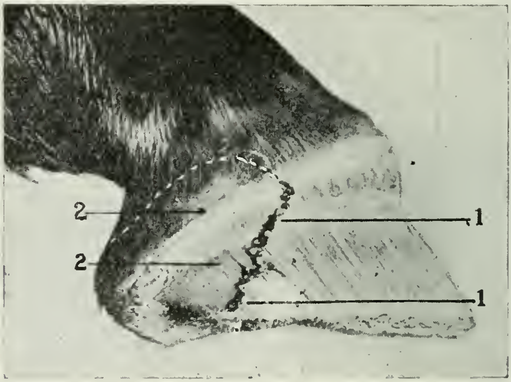

FIG. 252.—THE RIGID AND YIELDING PORTION OF THE FOOT.

1, 1, The line of the lateral cartilage, ascertained by passing pins through the laminæ into the junction of the cartilage with the bone; 2, 2, the portion of the vascular wall, coronary body, and skin covering the lateral cartilage. The part of the lateral cartilage extending above the hoof has its upper edge outlined, but the dotted line is too straight (see Fig. 232).

The folding up of the horny and vascular leaves in the foot, in the manner previously described, has another function besides that of merely supporting the weight and rendering the union firm. Reference has previously been made to the remarkably small size of the horse's foot in proportion to the size of his body.

In a comparison of the horse's foot with the human foot, the advantage, so far as size is concerned, in the majority of cases lies on the side of the biped. The most interesting fact which physiology has to demonstrate is that, though the foot presents a small surface, in reality it encloses a vast area, due to the anatomical arrangement of the laminæ. It is clear that by the process of folding up material within, the surface of the foot is considerably increased. In other words, by this arrangement the foot has been kept within small proportions without affecting its strength. A book, say of 600 pages, may, by placing one leaf on the other, be made to occupy a bulk represented by a few inches; but if each page be laid out separately on the ground, and made to touch the others, the surface covered will be considerable. This is exactly what occurs in the foot; the insensitive and sensitive leaves by their singular arrangement increase the surface of the foot, and yet keep it within reasonable limits. Bracy Clark, one hundred years ago, was the first to recognise this provision, and had a calculation made as to the increased surface afforded, which was considered to be equal to 1½ square feet. Moeller* has estimated that it is equivalent to 8 square feet, whilst Gader's estimate† is 10¾ square feet. For safety Moeller's number is adopted. The bearing surface afforded by each foot is equivalent to 8 square feet, giving a total area of 32 square feet. It is evident that, as feet vary greatly in size, this surface must accordingly be greater or less.

The physiological function of the leaves of the foot is demonstrated by pathological observation. Inflammation of the laminæ, apart from septic or intestinal poisons, occurs either through severe work or through an animal standing too long in one position; in either case the parts get strained. The practical value of exercising horses which from any cause have to stand for a length of time is well known; exercise overcomes the tendency of the laminæ to congestion from continual strain, and the feet not only become cool, but the animal may continue standing for a considerable time if exercised daily. The treatment of laminitis by exercise possesses a sound physiological basis.‡ If any doubt exists as to the function of the laminæ in supporting the weight of the horse's body, it is only necessary to look at the processes which occur in them as the result of disease. Laminitis is often attended by separation of the laminæ, when, the horse's weight being no longer properly supported, the pedal bone under the influence of the body weight is actually forced through the sole of the foot.

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* *Op. cit.*

† Goubaux and Barrier, 'Exterior of the Horse' (translation).

‡ This treatment has been known for at least 1,000 years.

The Use of the Bars.—As we have previously mentioned, the portion of the wall known as the 'bars' runs forward under the foot instead of completing the circle of the wall. The object of this non-completion of the ring the wall originally gave promise of forming, is to allow of expansion of the foot by making room for the elastic posterior foot—viz., the plantar cushion and foot-pad. The explanation why the wall turns in instead of ending abruptly is that it thus affords a solid bearing to the posterior part of the foot, gives additional strength, and secures a more intimate union with the sole. The bars, being part of the wall, are intended to bear weight, and in consequence in the foot of the wild horse and zebra they present the most extraordinary development.

The **Use of the Sole** is quite clear: it is to afford protection to the sensitive parts above. Its normally concave shape (Figs. 243 and 244) proves that it is not intended to bear on the ground over its general surface, and the acute lameness which results from a stone in the foot gives further proof, if any were required, of its indifferent weight-supporting properties; that margin, however, in contact with the wall can bear weight, as there is no sensitive part immediately above it (see Fig. 244, 6). Under the influence of the body weight the sole becomes slightly flatter, especially that portion of it situated posteriorly in the horns of the crescent (see p. 716). When the expansion of the foot is studied, the object of this flattening will be more apparent.

The Use of the Foot-Pad.—This is one of the chief anti-concussion mechanisms in the foot; it exists to prevent jar, and it does so by receiving, in conjunction with the posterior wall, the impact of the foot coming to the ground; the shock is imparted to the plantar cushion, and through the lateral cartilages to the wall of the foot, which bulges or, as it is termed, expands (see Fig. 253). In breaking the jar (not only to the foot, but to the whole limb), it is assisted by its elastic, rubber-like nature. For its perfectly healthy condition the foot-pad needs contact with the ground; it is strange that two structures situated side by side—viz., the sole and the pad—should be so opposed in this respect. If the foot-pad be kept off the ground, the part atrophies, the heels contract, the foot is rendered smaller, and the pad becomes diseased. This wasted condition of the pad and narrow foot may be remedied by pressure, but that pressure must be ground pressure. It is possible by means of a bar-shoe to throw considerable pressure on the pad and heels, but the foot still contracts; it is only when the pad is bearing on the ground that it continues in a healthy condition, and retains its normal size. Foot-pad pressure is, therefore, one of the rules in shoeing if the part is to be able to exercise its natural functions. In thinking of the foot-pad as a buffer, sight must not be lost of the fact that it affords protection to the joints and flexor tendon of the foot, matters of vital importance. The position of these relative to the foot-pad is seen in Fig. 233.

Use of the Lateral Cartilages.—Those functions of the lateral cartilages which have already been referred to may be summarised as follows: These structures form an elastic wall to the sensitive foot, and a surface of attachment for the vascular laminæ; they also admit of increase in width occurring at the posterior part of the foot without destroying the union of the two sets of leaves. Further, by their connection with the vascular system of the foot, their elastic movements materially assist the circulation. The primary use of the lateral cartilages is to render the internal foot elastic, and to admit of its changes in shape which occurs under the influence of the weight of the body. The

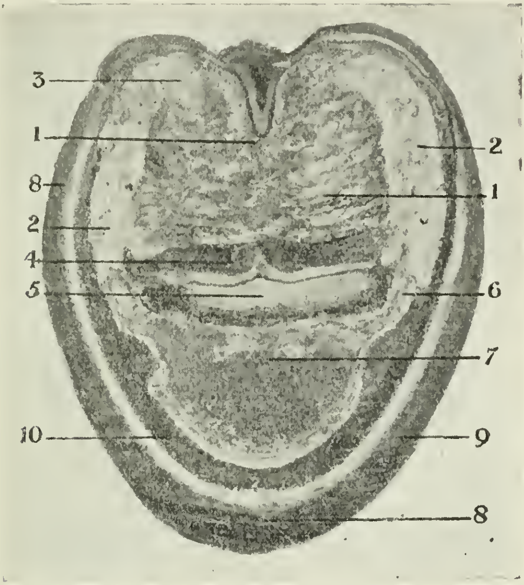

FIG. 253.—HORIZONTAL SECTION ACROSS THE STRUCTURES OF THE FOOT PARALLEL TO THE GROUND AND TWO INCHES ABOVE IT.

The plantar cushion, 1, 1, practically occupies half the foot, and is lodged between 2, 2, the lateral cartilages: these may be seen extending forward and attached to the wing of the pedal bone at 6; they end posteriorly at 3, fusing with the plantar cushion; 4, cut surface of perforans tendon; 5, cut surface of the navicular bone; 7, the pedal bone; 8, the white line, extending around the wall from heel to heel; 9, the wall: note the difference in thickness between the toe and the heel; 10, the vascular laminæ.

alteration in the shape of the foot is brought about by pressure on the pad, which widens and in consequence presses on the bars. The pressure received by the pad is also transmitted to the plantar cushion, which likewise flattens and spreads under pressure. Both of these force the cartilages slightly outwards. When the posterior wall recoils, the cartilages are carried back to their original positions. Should this elastic cartilage under pathological conditions become converted into bone, its functions are destroyed and lameness may occur. It has been demonstrated by the writer that by surgical interference the hoof can be made permanently wider, and thereby rendered capable of accommodating lateral cartilages which have undergone an increase in size as the result of ossification.*

Anti-Concussion Mechanism.—The special physiology of the foot is a consideration of the factors whereby the parts are saved from concussion, in spite of wear and tear, batter and jar. The weight carried on each fore-foot when the horse is standing is rather more than one-quarter the weight of the body; during locomotion the amount varies from half the weight in the trot to the entire weight in certain stages of the canter and gallop. The mechanisms which exist in the foot to save concussion are intended not only for the protection of the foot, but also to save the limb, and they may be tabulated as follows:

1. The yielding articulation in the pedal joint.
2. The increase in the width of the foot when the heels come to the ground, known as expansion.
3. The elastic foot-pad.
4. The slight descent of the pedal bone, and with it the sole.

Expansion is a term warranted by custom, though perhaps not free from objection. It indicates the fact that when the weight comes on the heels, the foot becomes wider opposite to them (Fig. 254). The increase in the width of the foot is due to a temporary alteration in the shape of certain of its structures. As a matter of fact, an increase in the width is not the only change which occurs; it can be shown that the heels at the coronary edge sink closer to the ground, while the coronary edge of the wall in line with the toe of the foot retracts, or travels backwards and downwards (Fig. 255, A). In all fast paces, when the foot comes to the ground, the posterior wall and foot-pad first receive the weight. Under the influence of the body weight the foot-pad, as we have seen, is compressed and becomes wider; the plantar cushion with which it is closely in contact is also compressed and becomes wider. The effect of this increase in width is that the foot-pad presses on the bars, while the plantar cushion presses on the cartilages, both of which, yielding laterally, force outwards the wall at the heels (Figs. 254 and 255, B). When the weight is taken off the foot, the heels return to their original positions, and the foot becomes narrowed. The increase in width which the foot undergoes is very small indeed; this is probably the reason why for years its existence has been disputed, especially in this country.[*] The employment of delicate apparatus such as those used by Lungwitz[†] and by the writer[‡] (Fig. 256), and experiments upon feet which have not been mutilated in shoeing, have placed the subject beyond all doubt.

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* 'Operation for the Cure of Lameness arising from Side-Bone,' *Veterinary Journal*, vol. xxv., p. 393, 1887.

The area over which the wall expands can be seen in Fig. 255, A; the shaded portion of the heel represents the part which yields laterally. At times expansion is registered at the coronet, and little or none on the ground surface, but as a rule the amount obtained at the coronet can also be obtained near the ground. As to the amount of expansion no definite statement can be made; it is small and is influenced by the shape of the foot; horses with low heels and full, well-developed foot-pads register a larger amount than those in which the heels are high and rigid. The measurements obtained by the writer with very delicate apparatus were smaller than those obtained in Germany by Lungwitz. On an average there was obtained, by simply lifting up one fore-foot, and so causing the horse to throw double weight on the other limb, an expansion of $\frac{1}{50}$ of an inch for one-half of the foot, or $\frac{1}{25}$ of an inch total increase

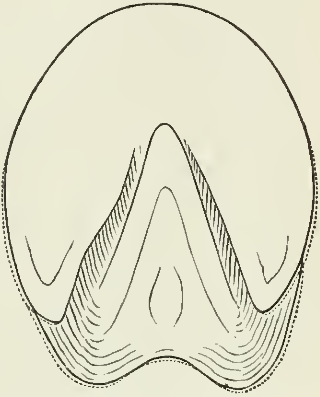

FIG. 254.—DIAGRAM TO ILLUSTRATE THE EXPANSION OF THE FOOT (LUNGWITZ).

The unbroken outline illustrates the shape of the foot at rest; the dotted outline shows the portion of the foot which has yielded laterally under the influence of the body weight.

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[*] Nevertheless, Bracy Clark demonstrated it over one hundred years ago. He says: 'The term "elasticity," however, by its exercise and use will explain, like the principles of gravitation in the hands of the astronomer, nearly everything that before was dark and obscure in the arts of the foot.' W. C. Spooner ('Treatise on the Foot and Leg of the Horse') stated in 1840 that the expansion of the foot was equal to $\frac{1}{12}$ of an inch.

[†] *The Journal of Comparative Pathology and Therapeutics*, vol. iv., p. 3, 1891.

[‡] 'The Apparatus Employed in Inquiring into the Physiology of the Horse's Foot,' *Veterinary Record*, vol. iv., p. 263, 1891.

in width. Naturally, during locomotion a greater expansion than this occurs. The question may be asked, What advantage

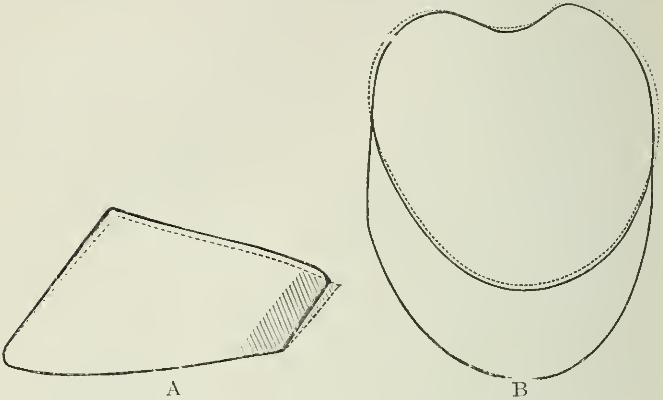

Fig. 255.—Diagrams to show the Area over which the Wall expands, and to illustrate the Retreat of the Anterior Coronary Edge of the Hoof, and the Sinking of the Heels (Lungwitz).

A, The unbroken outline shows the shape of the foot with no weight on it; the dotted outline illustrates the retreat of the coronary edge in front and sinking of the heels. The shaded part illustrates the area which expands.

B, In this figure the hoof is looked at from above; the unbroken outline is the coronary edge from heel to heel. The dotted line shows the change in shape it undergoes under the influence of the weight of the body.

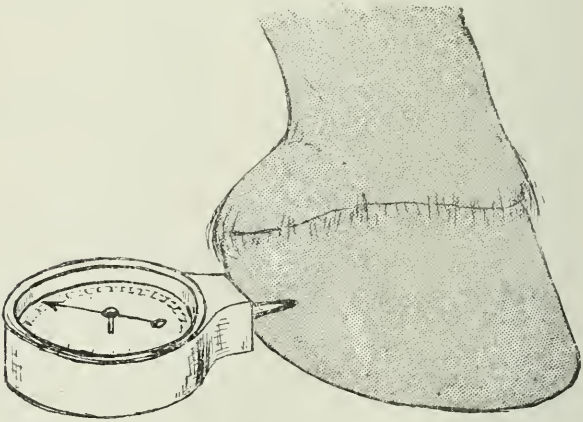

Fig. 256.—Apparatus for Measuring Expansion of the Foot.

The gauge is adjusted to different levels of the wall by means of a block; it registers from $\frac{1}{350}$ to $\frac{1}{25}$ inch.

can be gained by such a small increase in the width of the foot? Small as the increase is, it still makes all the difference between a yielding and an unyielding block of horn being brought to the ground; it 'gives' instead of offering resistance, and this 'give' is sufficient to prevent the hoof from being fractured, while the pad which has largely caused the expansion has acted as a buffer and assisted to destroy concussion.

There is no point in the physiology of the foot which has given rise to greater diversity of opinion than the question of 'expansion'; modern investigations completely support the views of the earliest observers. The retraction of the coronary edge of the foot in front and the sinking behind are accompanied by a tense condition of these parts which, since the days of Bracy Clark, have been regarded in the light of an elastic ring or support to the pedal joint. The tense condition is due to the change in the shape of the coronary edge, but whether this is capable of affording support is not evident.

In addition to the changes in the coronary edge of the foot during the period of expansion, another condition is present—namely, *compression* of the wall under the influence of the body weight, which produces a diminution in its height. This can be roughly demonstrated in the following manner: If a portion of the wall at the heel be cut away so as just to clear the shoe when the latter is fitted, it will be found on placing weight on the limb, by lifting up the opposite fore-foot, that the wall has descended sufficiently to touch the shoe. The experiment may be rendered less free from objection by removing a piece of the wall, as in Fig. 257. If this is made sufficiently large to admit a penny when the foot is off the ground, the coin cannot be introduced into the slot when the weight is placed on the foot. The only explanation which can be afforded is that given above—viz., the wall has undergone sufficient compression to allow the part which was originally clear of the shoe to come in contact with it, and to do this it must have diminished in height.

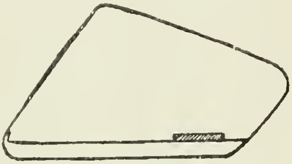

Fig. 257.—Experiment for Ascertaining the Compression of the Wall.

The **Descent of the Pedal Bone** is the last factor employed in saving concussion. The existence of this has been as strenuously denied as the expansion of the wall, but there is, however, no difficulty in demonstrating it; the value of such a movement is undoubted. Concussion to the sensitive foot is prevented by a slight up-and-down play between the sublaminal tissue and the pedal bone; as the weight comes on to the foot the pedal bone descends slightly, to rise again when the weight is taken off the limb.* As the pedal bone descends, the sole on which it is resting also descends slightly and comes nearer to the ground (p. 726); this is one reason why the sole is concave instead of flat. The soft horn uniting the sole and wall (p. 716) specially provides for the slight descent of the sole. The descent of the internal foot saves concussion, in the same way that it is easier to catch a cricket-ball with a retreating movement of the hand than by rigid opposition. Its movement also facilitates the circulation. The descent of the pedal bone is a most important physiological factor, and one of the safeguards of the sensitive foot.

Vascular Mechanism.—Situated as the foot is farthest from the heart, it is natural to inquire how it is that the blood is able to circulate through it so thoroughly, and whether some means are at hand for assisting the force of the heart in facilitating the circulation. Though the contraction of the left ventricle is sufficient under ordinary circumstances to bring the blood back to the right side of the heart, it is doubtful whether it would be wholly sufficient to empty the foot of blood and keep the considerable plexus of veins full. This plexus is shown in Fig. 240 (p. 711), which is a reproduction from a photograph of a corrosion injection.† The figure conveys very accurately an idea of the remarkable venous arrangement of the foot. The venous circulation is assisted by two movements in the foot—viz., the expansion and recoil of the outer foot, and the descent and elevation of the inner foot. There is no difficulty in seeing the movement imparted by locomotion to a column of fluid circulating in these parts, for if a plantar vein be divided and the horse made to walk, every time the foot comes to the ground the blood spurts out from the vein as if from an artery; when the foot is taken off the ground, the stream of blood becomes greatly reduced. A perfect pumping action is in this way produced. The mechanism can also be demonstrated on the dead limb by placing a manometer tube filled with water in each plantar vein, and then pressing downward on the limb, thus roughly imitating the weight coming on to the leg. The water rises in the manometer tubes with every compression of the foot, and falls during the period of no pressure, a period corresponding in the living animal to that during which the foot is off the ground.

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* Eighty years ago W. C. Spooner wrote: 'On trying the elasticity of the membrane which connects the laminæ to the bone, I found, somewhat to my surprise, that it yielded considerably when pulled downwards and very slightly when pulled upwards' (*op. cit.*).

† The figure appeared in an article by Dr. C. Storch, of Vienna, on 'The Venous System of the Horse's Foot,' *Oesterreichischen Monatsschrift für Thierheilkunde*, 1893.

We must accept, therefore, as a proved fact that the venous circulation is largely facilitated by the expansion and contraction of the posterior part of the foot; during expansion the blood is being driven upwards, and during recoil it is aspirated by the veins. Indeed, so perfect is this mechanism that there are no valves in the veins of the foot, and none are found nearer than the middle of the pastern. To assist the circulation to the utmost, the large venous trunks at the postero-lateral part of the foot are in close connection with the lateral cartilages, and some of the vessels even pass through their substance.

A summary of the physiological features counteracting concussion and facilitating circulation may be stated as follows:

When the weight comes on to the foot, it is received by a yielding foot articulation, an elastic wall, an india-rubber-like pad, and through these by the plantar cushion. The elastic posterior wall is pressed outwards by the compressed pad and plantar cushion, and it expands slightly from the ground surface to the coronet. At the moment of expansion the bulbs of the heel of the foot at the coronary edge sink under the body weight and come nearer the ground, and as a result of this the anterior coronary edge retracts. The pedal bone descends slightly through its elastic connection with the sensitive laminæ, and presses the sole down with it, while the wall of the foot slightly diminishes in height owing to the compression to which it is subjected. Under these conditions the blood-pressure in the veins of the foot rises, and the vessels are emptied. When the weight is removed from the foot the bloodvessels fill, the pad and posterior walls recoil, the bulbs of the heel rise, and the foot becomes narrower from side to side; at the same time the anterior edge of the coronet goes forward, and the pedal bone and sole ascend.

The **Nervous Supply** of the foot was mainly worked out by Mettam.* Tactile sensibility had long been known to exist, but the nature of the end organs concerned was unknown He has shown that these partake of the character of Pacinian corpuscles, arranged sometimes singly, sometimes in groups, and with other positional modifications, which has enabled four distinct methods of distribution in the plantar cushion to be recognised. Pacinian corpuscles have also been recognised in the vascular laminæ and in the skin of the coronet and heel. Valuable as this nerve-supply is in keeping the animal informed of the nature of the ground travelled over, yet it is not essential to progress or safety. All sensory impulses may be cut off from the feet without interfering with the safety of the animal (p. 615). The inner foot is acutely sensitive to touch, especially the vascular tunics. The plantar cushion is not nearly so sensitive, although Mettam has shown that it is liberally supplied with touch organs.

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* *Op cit.*

Physiological Shoeing.—It is impossible to conclude this chapter on the foot without some mention of what may be termed 'physiological shoeing.' By bearing in mind the functions of the various parts of the foot, we can confine the evils connected with shoeing within comparatively narrow limits. The following rules form the basis of physiological shoeing:

1. The reduction of the wall to its proper proportions, such as would have occurred through friction had no shoe been worn.
2. Fitting the shoe accurately to the outline of the foot, and not rasping away the exterior of the crust to fit the shoe, since this not only renders the horn brittle, but causes much loss of bearing surface.
3. The exterior of the wall should be left intact. The practice of rasping the wall for the *sake of appearance* destroys the horn, and allows of such considerable evaporation from the surface of the foot that the part becomes brittle.
4. The sole should not be touched with the knife; it cannot be too thick, as it is there for the purpose of protection.
5. The bars should not be cut away; they are part of the wall, and intended to carry weight. The shoe should rest on them.
6. The foot-pad should not be cut, but left to attain its full growth. No foot-pad can perform its functions *unless on a level with* the ground surface of the shoe.
7. The pattern of shoe is immaterial so long as it has a true and level bearing, and rests on both the wall and bars. The simpler the pattern of shoe, the better. Its weight should be regulated by the class of horse, and calculated to last a month.
8. A shoe can be fitted cold, but it is not so satisfactory as hot fitting, which insures perfect adaptation between the shoe and the foot. The heat employed in fitting should not scorch the sole; the shoe should be at a 'black' heat, and the wall must not be roasted.
9. The shoe should be secured with as few nails as its size admits. No more nails should be used than are absolutely necessary, as nails destroy the horn; further, they should not be driven higher than needful, for high nailing is ruinous to feet.
10. The 'clips' should be laid evenly, and not driven violently into the wall.

Such, briefly, are the conditions which fulfil physiological shoeing. The vicious and senseless practice of cutting away the horn of the foot-pad and sole, and of thinning the wall by rasping it, are the abuses of shoeing, and are capable of control. The real physiological evil in shoeing, and one which cannot be remedied, is the driving of nails into the foot (see p. 735, Evulsion).

Pathological.

The diseases affecting the foot of the horse are numerous, and as a rule serious; they may be connected with the vascular supply, with the bony foundation, with the cartilages and structures around the coronet, with the joint, or with the external cover. **Laminitis** and **Navicular Disease** have been previously touched upon in their physiological bearing. **Ossified Cartilages** have been referred to in connection with the lateral cartilages. **Fistula of the Coronet** is serious, owing to its proximity to the pedal joint, and its affecting non-vascular structures like the lateral cartilage; the process is destructive and repair slow. **Suppuration** around the coronet is a formidable affair; the parts allow of very little swelling, are rigid and unyielding, and burrowing of pus occurs such as is hardly met with elsewhere. It is the dread in all foot injuries, and is due to the manner in which the parts are confined within an unyielding box. There are few diseases more painful, and few of which the surgeon has more genuine dread. Suppuration may follow any injury, from an injury in shoeing to a tread on the coronet. **Injuries in Shoeing** are generally caused by a heel nail, occasionally by the foot being over-reduced. A shoeing injury causes intense pain, and, if severe, is followed by considerable destruction within the foot. A frequent injury in the angle between the bar and wall is caused by the heel of the shoe, and known as **Corn**; it is due to sole pressure, which in this region especially cannot be tolerated. It is a bruise of the part which is very persistent, and frequently permanent. It has a physiological basis; the foot grows forward (p. 723); it carries the shoe forward, and so takes it off the bars. The heel of the shoe then beds itself into the angle formed by the sole between the wall and bar. **Bruise of the Sole** may occur at any other part of the sole, but is never followed by permanent results, as is a corn. The sole cannot withstand pressure, especially that caused by a stone becoming wedged between the foot-pad and the shoe. **Arthritis** from penetrating wounds of the foot is common, but the pedal joint does not suffer from locomotive arthritis, as does, for instance, the joint immediately above it, and many others in the body. Nor do the foot-joint or tendons suffer from sprains, though, under the influence of erosion after neurectomy, the tendon in navicular disease may be worn through and snap, or even the bone fracture. **Fracture of the Pedis,** in spite of its porous nature, is very rare. When it does occur, the bone rarely unites, though the parts are contained in a permanent splint, which, theoretically, should lead to perfect union. The fact, however, is that, under the influence of the body weight, the fragments are always being forced apart. Nutritive changes occur in the foot after neurectomy, and the hoof may come off, or so-called **gelatinous degeneration** of the foot and limb occur as high as where the nerves are divided. **Evulsion** of the healthy foot may occur as the result of an accident, the foot being caught, for instance, in railway-points, and the animal, in its struggles, pulling the inside foot out of its cover. In these cases the nails in the wall have such a powerful hold that, rather than allow the shoe to tear away, the hoof is pulled off—an object-lesson in the security afforded by nails, and the hopelessness of ever attaching the shoe by any other means so simple and effective.

A weak wall in the fore-foot is liable to fracture during dry and hot weather; this is known as **Sand-crack,** and its physiology will be understood when the necessity for moisture in the horn is borne in mind (p. 721). The crack always begins at the coronet; it opens and closes in accordance with the expansion and recoil of the foot, and demonstrates these movements. Sand-crack in a hind-foot is a totally different matter; it occurs at the toe, extends from bottom to top, and is due to violence, especially in heavy draught. **Contraction** of the foot was the great bugbear in days gone by. It was regarded as a disease; in the present day it is looked upon as a symptom. A foot will contract if it is rested, as in navicular disease, and the cause of this must be evident from what has been said in the previous pages. If the foot-pad be cut away in shoeing and no pressure given it, contraction occurs as a result, in consequence of loss of function of the food-pad and plantar cushion. Inflammation of the glands of the plantar cushion leads to an offensive discharge known as **Thrush,** which erodes what is left of the horn of the foot-pad. This condition is aggravated by dirt, and is therefore common in the hind-feet, but its chief cause is a want of proper foot-pad pressure. The horn of the sole and foot-pad, from causes which are not clearly known, but are probably microbic, takes on an unhealthy, cheese-like, and offensive condition, due to disease of the horn-secreting membrane of these parts. It is a most intractable disease, known as **Canker,** and is frequently associated with defective hygienic care. The layer of white horn at the toe between the insensitive laminæ and the outside wall is liable to a curious disintegration known as **Seedy Toe,** which, by extension, may excavate the wall nearly as high as the coronet. It is a slow process, and recovery is tedious. The hoof frequently shares in any general disturbance of the system. There is a tropical form of skin disease in which the hoofs frequently indicate by the scaly condition of the wall that the horn-secreting substance—a modified skin—is sharing in the general disorder. Similarly, the growth of the feet may from constitutional causes be temporarily inhibited, and then start again with renewed vigour, every increase in the production of the wall being marked by a ring which extends all round the hoof. Horses exposed to standing in wet places like marshes have an impetus given to the growth of the wall, resulting in rings on the feet.

The above indicates the numerous diseases or injuries to which the foot is liable. The foot has a special pathology, as well as a special physiology. It is the most common seat of incurable lameness, and has always been so since the horse was domesticated. 'No foot, no horse,' is as old as the days of Xenophon. This horse-master tells us how to keep the horn of the feet of cavalry horses. hard—a very necessary matter at a time when shoes were unknown. It is a remarkable fact that the horn of unshod feet is infinitely harder than that of horses wearing shoes. It may, indeed, be so hard as to resist the entry of a nail.

CHAPTER XVIII

GENERATION AND DEVELOPMENT*

SECTION I.

THE differences in anatomical arrangement of the generative organs of the various domesticated animals may be briefly noted. They are very remarkable, and afford an object-lesson in the methods by which identical physiological results may be obtained by very diverse anatomical structures.

The *horse* is the only domesticated animal which in the general arrangement of the generative organs resembles man. The penis is provided with a large amount of erectile tissue, but the glans differs; there is a fossa around the opening of the urethra, and the latter projects by means of a short tube. The corona, also, during the orgasm swells enormously, resembling, as described by Chauveau, the rose of a watering-can. The penis of the horse is capable of being retracted within its sheath by means of an unstriped muscle running from the coccygeal vertebra as far forward as the glans. The retractor penis muscle is found not only in the horse, but in the ox, dog, and cat.

In the *ox* the testicles are relatively much larger than in the horse; they are also elongated, their long axes being vertical, whereas in the horse they are horizontal. The penis possesses very little erectile tissue, a fibrous core largely replacing the usual vascular tissue. In consequence, the organ is always rigid, and increases very little in size during erection. The penis is also doubled on itself, producing an **S**-shaped flexure effected by muscular agency. This flexure is obliterated during erection. The glans is small, pointed, and twisted, and in the twist the urethra opens by an extremely small side outlet. The prepuce, which internally is very narrow, runs much farther forward than in the horse; it has a pair of muscles to draw it forward over the glans and a pair to draw it back; both of these muscles are absent in the horse.

In the *sheep* the structures are much the same as in the ox, with the exception that the urethra terminates in a narrow spiral process, about 1½ inches in length, which comes off from the left side of the body of the glans. This appendage contains erectile tissue, and both it and the penis are rendered rigid by comprising in their structure a fibrous cord, which runs on either side of the urethral canal throughout the entire length of the organ.

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* In the preparation of this chapter several members of the profession have been good enough to afford me information on subjects which have not come under my personal observation. Some names are noted in the text, but I am also indebted to Lieut.-Colonel Head, Major J. Peddie, Messrs. H. Gray, H. Begg, R. J. Hickes, F. T. Harvey, P. Wilson, and J. Brown (of Invergordon).

In the *pig* the testicles are placed in the perineal region, the tail of the epididymis being very large. As in the ox, the penis possesses a sigmoid flexure; it has also a fibrous core and very little erectile tissue. The organ possesses no glans; it terminates in a corkscrew-like appendage of erectile tissue, in which the urethra opens by a slit. There are no muscles to the prepuce. Within the prepuce there is a diverticulum containing an offensively smelling mixture of decomposing urine, worn-out epithelium, and sebaceous material.

In the *dog* the testicles are placed between the inguinal and perineal regions, the long axis is oblique, and the epididymis large. This animal, as in carnivora generally, has a compound penis, the posterior part composed of erectile tissue, the anterior part formed of a bone covered with mucous membrane which forms a long, narrow, pointed glans, which in the dog is of considerable length, and extends over the entire length of the os penis (Sisson). Behind the elongated glans is a bulb. The bulb consists of erectile tissue, which, during intercourse, becomes enormously swollen; until the swelling subsides this bulb causes the organ to be imprisoned in the vagina.

In the *cat* the penis in a flaccid state turns backwards, as in the camel; in the erect condition it points forward. It possesses a small bone at the anterior part, and the membrane covering the glans is studded with erectile papillæ.

The *accessory generative organs* of the male also present differences. In the horse the *vesiculæ seminales* are not only a receptacle for seminal fluid, but are also glandular. In the ox they are wholly glandular. In the pig, also, they are glandular and very large; in the dog and cat they are absent.

In the horse the *prostate gland* connects with the urethra by a large number of openings; in the ox the gland is so small as to be frequently unobserved; it is also small in the pig, but large in the dog.

The *bulbo-urethral* (Cowper's) *glands* are well marked in the horse, and possess several excretory ducts; they are much smaller in the ox, and each possesses a single duct; in the pig they are very large, with a single excretory duct for each gland. In the dog they are absent.

There is much less to be said about the difference in the organs of generation in the females of different species. In all cases the uterus is two-horned. It is in one horn, and to a limited extent in the body of the uterus, that the fœtus is contained. In the case of twins one may be contained in each horn. In animals such as the pig, dog, and cat, both horns are occupied by fœtuses. The non-gravid uterus occupies the dorsal position in the abdominal cavity. On the other hand, the gravid uterus lies on the floor of the abdomen.

The uterus undergoes a great increase in length in consequence of pregnancy. In the mare, from about 16 inches in length it becomes 2½ to 3 feet when gravid; the empty uterus has a thick mucous membrane containing glands. The urethra is short and very distensible, a practical point in the extraction for calculus.

The ovaries of the cow are smaller than those of the mare, and the fimbriæ not so extensive. The body of the uterus is very short, the horns very long and spiral in their course; the muscular coat is thicker than in the mare; the mucous coat, especially of the horns, in both cow and sheep is studded with cotyledons, which during pregnancy become greatly enlarged; the cervix is very thick and rigid, the mucous membrane lining it being thrown into folds. In the pig the horns of the uterus are very long, repeatedly flexed on themselves, and possessed of great movement owing to the length of the broad ligaments. There is a long neck to the uterus, this and the vagina directly connecting without the intervention of an os uteri.

In the dog the ovaries and fimbriated extremities of the Fallopian tubes lie in a bursa. The horns of the uterus are long, narrow, and straight. In a gravid condition the horns are dilated for each fœtus with intervening constrictions, and the same remark applies to the pig and cat.

Descent of Testicles.—The testicles are intra-abdominal during the greater part of fœtal life; they gradually descend from the vicinity of the kidneys. A pouch of peritoneum grows down into the inguinal canal, carrying with it fibres of the abdominal muscles, which subsequently form the cremaster. Extending from the epididymis of the fœtal testicle to the bottom of what will become the scrotum is a cord known as the gubernaculum testis. It is this which, by gradually shortening its length, guides the testicle through the inguinal canal into its final position.

The testicles are normally in the scrotum of the foal at birth; they are sometimes temporarily withdrawn. Failure to descend is termed 'cryptorchidism.' Animals so affected may not be fertile, but in most other respects give every evidence of sex characteristics, and as a rule are most troublesome to deal with. In some animals—*e.g.*, the elephant and whale—the testicles never leave the abdominal cavity; in others they appear during the sexual season, and are withdrawn at its close, or the process of withdrawal may be voluntary. The horse is capable of exercising considerable retractile power owing to the size of the cremaster muscle.

Spermatic Fluid.—The portion of the testicle which secretes the semen is the seminiferous tubules; these are lined by several layers of cells which by the process of division result in the formation of spermatozoa. The first step is the production of *spermatogonia ;* from these, by division, are derived cells, known as *spermatocytes,* and from these in turn are formed *spermatids,* from which the *spermatozoa* immediately originate. During this process of cell division the head and subsequently the tail of the spermatozoon is formed. Masses of spermatozoa, with their heads to the wall of the tube and their tails to its central canal, may be seen in streams or clumps. Their development is assisted by other cells, known as those of *Sertoli*, a secretion from which is believed to furnish the spermatozoa with nourishment, and eventually enables them to turn in the lumen of the tube. During the process of development from spermatogonium to spermatozoon certain changes occur in the number of chromosomes; in the spermatid there is one-half of those found in the spermatocyte. The number of chromosomes in the body cells of a given species is definite (see p. 753); the reduction to one-half in the case of the spermatozoon (and also of the ovum, see p. 755) is preparatory to the union of these two cells; this union restores the full number of chromosomes to the body cells of the animal which results from their union. Spermatogenesis is associated with the production of nucleic acid, which is probably the material on which the cell proliferation depends. This nucleic acid is derived from lipoid granules furnished by the adrenal cortex. The store of lipoid in the testicle is contained in the cells of Sertoli.

The spermatozoa, having been formed, proceed along the ducts of the testicle and subsequently reach the epididymis. The epididymis is a secreting surface as well as a receptacle and conduit. It does not secrete semen, but it contributes to the production of a hormone, for animals in which a portion of the epididymis has been preserved in castration exhibit strongly marked male characteristics, even to the thickened crest, uncertain temper, and proud bearing. In the pig, an animal possessing a large epididymis, Iwanow has described energetic secretory activity as occurring here.

The tubules in the testicle are connected by an intertubular structure which contains the interstitial cells of *Leydig;* these cells provide the internal secretion of the testicle on which the secondary male characteristics depend for development, such as growth of mane, richness of coat colour, and, in ruminants, the growth of horns.

In all the higher animals the spermatozoa are tadpole-like bodies, propelling themselves by the flagellum or tail after leaving the testicle, but not, it is said, during the time they are within that organ. In the epididymis there is activity; here, as we have seen, the semen is to some extent stored, and during this time it is believed to undergo a process of 'ripening' under the influence of the secretion of this organ. This is supported by the undoubted fact that the seminal fluid becomes progressively poorer in fecundating properties and in number of spermatozoa in consequence of frequent coitus, there being insufficient time for ripening in the epididymis. The vitality of the spermatozoa inside the body of the female may be considerable; in the bat they remain alive for months, and then impregnate an ovum; in the hen all eggs are fertilised which are laid during three weeks succeeding the last act of copulation. Their period of life in the uterus of the pig is said to be brief. Lewis* states out of twenty-five sows the spermatozoa were alive in three cases after twenty hours, and in two cases at forty hours, and in all the other animals they were dead at the end of sixteen hours. On the other hand, living spermatozoa have been found in the uterus of the dog eight days after coition. Outside the body the vitality is a question of temperature and daylight. At a temperature of 13° to 21° C. 25 per cent. of the sperm cells of a stallion were alive at the end of six and a half hours (Lewis). Heape,* on the other hand, found in examining the fluid of a dog sent him by post that fully half of the spermatozoa were alive eighteen hours after being obtained. By keeping the fluid of the horse warm and in the dark it is said that it will retain its vitality for twenty hours; the addition of 5·2 per cent. solution of dextrose will keep it active for thirty to seventy hours (Sato). These facts have a practical application in view of the extension of artificial insemination.

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* *Oklahoma Experiment Station Bulletin*, 96. Quoted by F. B. Mumford, 'The Breeding of Animals,' New York, 1919.

The amount of seminal fluid ejaculated by different animals is dealt with at p. 759.

Spermatozoa are produced in enormous numbers; each cubic centimetre of human seminal fluid contains from 60,000,000 to 70,000,000 of cells, in the dog 45,000,000, in a vigorous stallion 42,800,000 (Lewis), but in the same animal, after very moderate stud demands lasting nine days (one service daily), the numbers had fallen to 7,430,000 per cubic centimetre.

The seminal fluid of animals differs in its physical characters.† All contain protein. That of the horse is rich in mucin and slightly gelatinous, but rapidly liquefies; it has a yellow, turbid appearance, and on being passed through the centrifuge this turbidity is not entirely removed, while the colour is unaffected; it has no smell other than that of urine; the proportion of fluid to spermatozoa is high. The sperm of the bull resembles that of the horse; in the ram the seminal fluid is an opaque, white liquid free from odour; in the dog it is turbid, greyish-white in colour, and free from viscosity or odour.

The Function of the Accessory Glands.—Spermatozoa find their way into the *seminal vesicles*, but whether these organs are mainly designed as receptacles is another point. The vesicle is undoubtedly glandular in structure, especially in the ox, and there can be no question that it adds a secretion of its own to the semen. This serves to dilute the semen, and may assist in maintaining the motility of the spermatozoa; but a gland measuring some five inches in length and two inches in width and thickness, as it does in the ox, is no doubt intended for other purposes, even though the dog and the cat are able to do without it. In castrated animals the glandular epithelium atrophies. In geldings Sisson records that he has found dilatation of the vesicles, which contained as much as a quart of thick, amber-coloured fluid. Between the seminal vesicles and the epididymis is the *vas deferens;* the mechanism by which the semen passes into the seminal vesicles is by no means clear. In the horse and ox the vas deferens and ejaculatory duct join and open by a common orifice. Sometimes in the horse these vesicles open into the urethra separately from the ejaculatory duct. In cases where the tubes unite the passage of semen from vas deferens to vesicula seminalis may be carried out by a closure of the ejaculatory duct, a reflux into the vesiculæ then occurring, but when each opens separately into the urethra, the flow of semen from vas to receptacle is difficult to explain.

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* 'The Physiology of Reproduction,' F. H. A. Marshall, D.Sc., 1910.

† This account is taken from E. Iwanow, *Comptes Rendus*, vol. lxxx., 1917.

On the vas deferens are certain swellings known as *ampullæ;* they are well marked in the horse and ox. It is in the ampullæ that the semen is stored while undergoing the process of 'ripening'; doubtless there is a secretion added to it from the wall of the ampulla itself, for the thickened secretion found in the epididymis becomes considerably diluted by remaining in the ampullæ.

The large seminal ejaculation of the horse and ox is largely stored up in the epididymis and vas deferens, and to a limited extent in the vesiculæ seminales; in the dog it is wholly held between the vas deferens and epididymis.

The secretion of the other accessory glands—*i.e.*, the urethral, Cowper's—and the prostate, remains to be considered. Iwanow suggests that the urethral glands furnish the first fluid in ejaculation, a clear liquid possessing bactericidal properties, for, as he says, it may be kept in unsterilized tubes for eight months without becoming turbid. He thinks its function is to wash and disinfect the urethral canal. The secretions of the urethral and bulbo-urethral glands and the *prostate* are added to the seminal ejaculation in the prostatic portion of the urethra. Cowper's secretion probably acts like that of the urethral glands; that of the prostate excites energetic movements of the spermatozoa. In the dog this gland furnishes the remarkable third ejaculation discovered by Iwanow which has yet to be dealt with. The prostatic secretion is more intimately connected with the sexual organs than those of the urethral and Cowper's glands. After castration the prostate atrophies, the other glands apparently do not. In ruminants the prostate plays a very unimportant part, the gland being insignificant in size.

The Ovum.—The main function of the ovary is to contain the ova and favour their development. It does not secrete them; the ova are laid down with the other cells of the body very early in the life of the embryo, a portion of material being set aside for their special development, as apart from the cells required for the construction of the other portions of the body. It is a very remarkable fact that within a few hours of the impregnation of the ovum, one of the first acts in the cellular scheme is to provide for the reproduction of the future animal, the prospective parent of which at this stage is a mere mulberry-like mass of cells. The germinal cells, as these are called, as distinct from the body or somatic cells, subsequently form an epithelial layer, which grows into the body of the future ovary as a long cylinder of cells; these are eventually cut off, and remain in the ovarian structure. At birth the ovaries contain some thousands of eggs, some of which in due course, as the period of puberty arrives, undergo further and more active changes. At this time the most advanced cells are enclosed in a follicle containing fluid, the *Graafian follicle.* Lining the follicle is a layer of cells known as the *membrana granulosa ;* at one part these are heaped up, known as the *discus proligerus* and within this mass the ovum lies buried. The Graafian follicle makes its way to the surface of the ovary, being enveloped in a two-layered cover formed from the stroma of the organ, known as the *theca folliculi.* The cells of the inner layer develop the yellow pigment, *lutein*, and subsequently, on the rupture of the Graafian follicle and the discharge of the ovum, secrete a yellowish pigment, which stains the cells filling up the gap left by the discharged ovum. As a result of the rupture of the Graafian follicle, a rent is made in the ovary. This wound generally fills with blood from the opened vessels, and for some time afterwards appears as a pigmented spot. If pregnancy has not supervened, it undergoes a retrogressive metamorphosis and soon disappears. If, however, the ovum is fecundated the *corpus luteum,* as this pigmented spot is termed, continues to grow, and may be observed in the ovary even near 'term.'

The **Corpus Luteum** of the pregnant animal is very much larger than that of the non-pregnant, and it appears to be conclusively settled that the existence of this yellow tissue in the ovary is not merely for the purpose of filling up a cavity in its structure; the yellow body is a ductless gland, which on pregnancy becomes an active secreting agent, producing a chemical substance (*hormone*) by which the ovum is anchored to the wall of the uterus, and its nourishment and development assisted. This ductless gland is functional until about the middle of pregnancy, when it is no longer a necessary factor in the fixation of the embryo and consequently degenerates. That the corpus luteum takes little or no share in the production of seasonal sexual excitement appears quite clear; as we shall see, this is the function of the stroma of the ovary, which pours an internal secretion into the blood, and so brings about menstruation (in primates) and œstrus. It has been stated that towards the end of pregnancy the corpus luteum produces a second hormone which helps to bring about involution of the uterus after parturition.

The mature ovum is very small ($\frac{1}{150}$ to $\frac{1}{120}$ of an inch), yet large enough to be seen by the naked eye. It is therefore one of the largest cells in the mammalian body, though infinitely smaller than the eggs of birds and reptiles. There is a mammal, the 'duck-billed platypus' (*Ornithorhynchus*), which produces eggs the size of a hazel-nut, and the ancestors of all mammals had eggs probably as large. The greater size of the eggs of reptiles and birds is due to the quantity of *yolk*, or *deutoplasm*, they contain, which in mammals is very small in amount, as the embryo of the latter is dependent upon the yolk-sac for nourishment only for a very brief period.

The ovum is a typical cell; it is spherical, more or less translucent, and contained within a membrane, the *zona pellucida*. The contents, or protoplasm, of the cell consist of fatty and albuminous granules, known as *yolk spherules*, and lying in the protoplasm is a nucleus, containing one or more nucleoli. The nucleus is spoken of as the *germinal vesicle*, the nucleolus as the *germinal spot*. One more body is found in the protoplasm, an *attraction sphere*, or *centrosome*. This latter is extremely small, but its functions are of the utmost importance.

When the rupture of the Graafian follicle occurs, the ovum is flushed out, and at the same moment, according to Hensen, the fimbriated extremity of the Fallopian tube becoming erect, grasps the ovary, and thus the escaping ovum is received into its 'duct.' Probably the converging furrows found on the plicated extremity of the Fallopian tube may assist in directing the ovum to the *ostium abdominale*. If by chance the ovum be not caught and carried away to the uterus as described, it may fall into the peritoneal cavity and perish; or if it has been already fertilised, abdominal fœtation may occur, the peritoneum acting as a matrix in which the embryo may develop. The method by which the ovum gains the Fallopian tube is not, however, settled. There is some evidence to show that it may be discharged into the abdominal cavity, and make its way into the Fallopian tube. The experimental introduction of small objects into the pelvic cavity has resulted in these being taken up by the tubes. In animals which have had one ovary removed the embryo has been found developed in the horn of the uterus on that side, though the ovum was derived from the opposite ovary. Even the ovary of one side and the uterine horn of the opposite side have been removed without interfering with conception; this indicates that the ovum may travel across the peritoneal cavity to the opposite Fallopian tube, and if, as Ewart states, the horse embryo is generally contained in the right horn, this must be of frequent occurrence in equines. Notwithstanding, the simple direct method of Fallopian tube grasping its own ovary appears the most reasonable explanation. In the dog special provision exists for the ovum to pass in this manner direct from the ovary into the Fallopian tube, for, as we have seen, the ovary and fimbria are in a capsule.

An ovum may fail to ripen and be discharged from the ovary; in this case it undergoes degeneration and atrophies. It is believed that this is liable to occur in underfed and in very fat animals, and Ewart draws attention to its occurrence in mares turned out during the winter. Freedom from sexual intercourse may also lead to degeneration of the ova, and probably explains the difficulty in getting old mares to breed.

Effect of Removal of Testicles and Ovaries.—In the chapter dealing with the endocrine glands reference has been made at p. 307 to the internal secretions furnished by the genital glands of both sexes; we are now in a position to consider in greater detail the internal secretions of the testicle and ovary.

If the genital glands are removed during early life or prior to puberty, profound changes occur in the organism. The secondary sexual characters are lost, the horse fails to develop a crest to his neck or the voice of the stallion (p. 154), his proud bearing and aggressive nature disappear, he becomes humble and submissive, his coat colour is never as rich as in the uncastrated animal, and a pure black horse becomes an impure black; pigment production, though not withheld, is modified. The ox lacks the massiveness, voice, and ferocity of the bull, and the flesh not only becomes tender, but is rendered palatable; there is also a disposition to accumulate fat (p. 379), a condition equally well marked in the sheep and pig, but absent in the horse, probably as the result of work. The change in the taste of the flesh of the sheep and pig is as well marked as in the ox. Such are the general changes resulting from the removal of the testicles. There are local changes; for instance, in the stag, if castration be performed in early life, the antlers never grow; if performed after the antlers are grown, these are shed from the seventh to the ninth day after operation, fourteen days being the longest time they remain.* If the epididymis be left, its presence modifies the growth of the next pair of antlers. We have already seen that the epididymis is a secreting gland, and noted its influence in the partial castration of horses (p. 740). If castration of the stag be practised on one side only, it is said—but the matter requires confirmation—that only the antler on that side is shed and fails to be reproduced.

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* H. Leeney, M.R.C.V.S. Communicated.

Though castration has no effect on the development of hollow horns, there is one ruminant, the *prong-buck,* that periodically sheds its hollow horns, and the effects of castration in this animal is to alter their direction of growth.

In horned sheep the effect of castration is to arrest the development of the horns, and they approximate to the type produced by the female (Marshall). Cocks converted into capons when young do not develop such full male plumage, and the combs and wattles are more like those of the hen. Crowing does not occur. If extracts of the testicle of the pig be injected the colour of the comb and gills is restored, crowing takes place, and the sexual instincts are re-established. When the injections are stopped the animal returns to its condition of capon (Pezard).*

Cats operated upon when very young have heads which are indistinguishable from that of the female; the tissues which give the head of the male cat its massive appearance are lost, and this may occur even when the operation is performed late in life (Leeney).

The removal of the ovaries brings about in women an artificial menopause; menstruation ceases, and there are characteristic alterations in features and body shape. There is not in the domesticated animals anything corresponding to the 'change in life' which occurs in women; animals may breed when extremely old, but the effect of removal of the ovaries is certainly to prevent the appearance of the œstral period, and ill-tempered mares have been benefited by the operation. It does not affect the secretion of the mammary gland in the cow, for animals in France are frequently 'spayed' when in full milk in order to keep them in this condition. In the sixteenth and seventeenth centuries in this country fillies were frequently operated upon within a few days of birth; there were complaints that this prevented their growth and development, which probably led to the abolition of this barbarous custom. The only animals regularly submitted to ovariotomy are pigs; it promotes early fattening and renders the flesh palatable.

Sexual Inversion.—It has been observed that secondary male characteristics follow the menopause in women, and in certain animals similar results have been observed. The cat ovariotomised in early life may develop a head of the male type; pullets from which the 'clutch' has been removed sometimes put on male plumage and spurs begin to grow; diseases of the ovary in hens or pheasants may lead to their crowing (Leeney).

Testicular and ovarian grafts have been inserted into castrated animals of both sexes with a certain amount of success. They, of course, act only by producing the *internal* secretion of these glands. If ovaries are grafted into young male rats after castration and testes into female rats after ovariotomy, the male shows motherly instincts in the protection and nursing of the young, and the female exhibits male instincts (C. R. Moore).*

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* *Physiological Abstracts,* vol. iii., 7.

The **Sexual Season** of female animals is a subject which has received exact expression from the pen of Heape,† whose communication, quoted below, we have followed in treating of this subject. Heape divides female mammals into two classes—*Monœstrous*, or those which have one œstrous period during the complete cycle, and *Polyœstrous*, or those having a series of œstrous cycles during the œstrous season. The first phase of generative activity at the beginning of a sexual season is known as *Proœstrum*, or the *proœstrous period*; it corresponds to the period 'coming on heat,' or 'coming in season,' and in the human female to the period of menstruation. The period lasts a variable time in different animals, and is succeeded by the *period of desire*, or *Œstrus*. It is only during this period that sexual intercourse is permitted, or that fruitful coition is possible. If conception does not occur or is prevented, œstrus is followed by *Metœstrum*, or the *metœstrous period*, during which sexual activity passes away, and is succeeded by a period of complete rest or freedom from sexual excitement, known as *Anœstrum*. The anœstrous period may last two, three, eleven, or more months, depending on the species.

The sexual cycle is not always as above described; there are animals in which metœstrum is not followed by a period of complete rest, but by a short quiescence, known as *Diœstrum*, which lasts a certain number of days and is then followed by a new proœstrum, œstrus, metœstrum, and diœstrum. Among monœstrous mammals is the wolf, which in the wild state has only one sexual season in the year. Another is the dog, though in this case the sexual season recurs during the year, but the periods in each case are quite distinct, and followed by complete rest, which is the essentially distinguishing feature. Among polyœstrous mammals are the mare, cow, sheep, pig, and all of these during a portion of the year exhibit a series of diœstrous cycles (in the absence of pregnancy), followed by anœstrum until the next year. The number of annual sexual cycles which any given species passes through is vastly influenced by domestication. Probably in all primitive species one sexual season yearly was the rule. Domestication alters this. The abundant food supply renders the struggle for existence no longer acute, the dread of being preyed upon by the enemies peculiar to each species is removed, and one of the responses to these altered conditions is a greater desire to multiply, for the reason that the energies previously expended in the struggle for life are turned into a fresh channel. The cat in a wild state has one sexual period a year; the domestic variety has three or four. The wild dog and wolf breed once annually, in captivity twice annually. The lioness in a wild state has probably but a single breeding season; in captivity the œstrous period may recur three or four times a year. Bears in a wild state have a single breeding season, in captivity more than one. The wild otter has a single season, but in a state of captivity she comes ' in season ' every month (Marshall and Jolly). So far, in fact, as evidence is available, a single sexual season for animals in a state of freedom appears to be the natural condition, *polyœstrum* being an acquired character. The frequency of œstrus under domestication is essentially influenced by food, temperature, and environment.

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* *Physiological Abstracts*, vol. iv., 3.

† 'The Sexual Season of Mammals,' etc., by W. Heape, M.A., *Quarterly Journal of Microscopical Science*, vol. xliv., p. 1, 1901.

The complete œstrous cycle in the **dog*** under domestication is six months. Every six months, in spring and autumn, the majority of dogs come ' on heat,' though there are many exceptions to this rule, some of the smaller breeds of dogs having a three and four heat period in the year. The period of proœstrum lasts from seven to ten days, and œstrus lasts another week.

In the **mare** the complete œstrous cycle, with its diœstrous intervals, may last for months, in the majority of mares from February to June or July; and unless the mare is rendered pregnant, the diœstrous periods last twenty-one days, and are followed by proœstrum, œstrus, etc., as previously described, though the time-duration of these is irregular, generally brief, and always uncertain. For instance, the exact period at which the mare is ripe to receive the male may only be a matter of a few hours, whereas she may be several days in a highly unsettled sexual condition. The mare is in a condition of œstrus on the seventh to tenth day after foaling; in thoroughbred mares it may be the sixth. At this period, though still nursing, she desires intercourse, and in this respect differs from the nursing cow and sow. If she does not conceive, the period of diœstrum is twenty-one days, and is followed by œstrus, the returning heat usually lasting longer by two or three days than the original ' heat.'

The **cow** under domestication will breed at any time of the year. She ordinarily takes the bull six weeks or two months after calving, but it is unusual for her to accept the bull while suckling her calf. If the latter be removed or weaned, she shows signs of œstrus six or seven days later, the duration of which may be twelve hours. The period of diœstrum is twenty-one days, at the end of which time both cows and heifers exhibit œstrus. This cycle continues until they are settled in calf.

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* ' Contribution to the Physiology of Mammalian Reproduction.' Part I.: ' The Œstrous Cycle in the Dog,' by F. H. A. Marshall and W. A. Jolly, *Phil. Trans.*, B, vol. cxcviii., 1905.

With **sheep*** œstrus may only last one or two days, or it may pass away very quickly, the diœstrum which follows lasting from thirteen to eighteen days. The number of recurrent periods in any one cycle in the sheep has been observed to depend upon breed; two, three, or four recurrent periods have been noted. There are some breeds of sheep which may produce two sets of lambs in one year. The period of œstrus may be induced almost at any time in the late summer and autumn by the introduction of the ram to the ewes (Goodall).

The **sow** takes the boar about a week after she has weaned her litter, or about eight weeks after farrowing. The period of œstrus lasts about two days, the diœstrous period twenty-one days.

The only known animal which in a wild state exhibits a continuous series of diœstrous cycles is the monkey, but even in this case the season is limited at which conception is possible (Heape).

By systematically preventing animals from breeding, the sexual season may be interfered with to the extent of complete cessation (Heape). Certainly the mare used late in life for breeding purposes often proves barren. Yet there are mares which, though deprived of the services of the male, never lose their desire, and may for the greater part of their lives be a source of danger from sexual excitement.

Cause of Proœstrum and Œstrus.—The œstrous period may appear in the dog after a portion of the spinal cord has been excised, proving that it is a process quite independent of the nervous system, that it may exist in the absence of consciousness on the part of the animal, and that its production is under no central control. Furthermore, an animal so operated upon may become pregnant and be delivered in the ordinary way, though quite unconscious of the process. Heat and menstruation are produced as the result of an internal secretion derived from the *stroma* of the ovary. It is possible with some animals—for example, sheep—to hurry forward the œstrous cycle by liberal feeding; similarly, it may be retarded or the cycle shortened

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* 'The Œstrous Cycle and Function of the Corpus Luteum in the Sheep,' by F. H. A. Marshall, B.A., *Phil. Trans.*, B, vol. cxcvi., 1903.

(mare) by poverty of keep, but these are merely features of general metabolism; the real factor is the chemical secretion of the ovary.

The *External Signs of Procœstrum* in all domesticated animals are a swelling of the vulva, more or less pronounced, and a slight flow of mucus, which may be blood-stained. This is the only approach to the condition of menstruation in women. There is excitement. The mare may refuse to work, squeals and kicks when approached, elevates and protrudes the clitoris, and micturates frequently, the material being very mucoid. The cow bellows, is excited, and mounts its fellows. Sheep become restless and follow the ram. The dog is playful, excited, and desires the attention and companionship of the males of her own species. In all animals it is only during the actual period of œstrus or desire that copulation is permitted, and in all polyœstrous domestic animals this period is variable in duration; it may be a day or two, or a few hours only.

Changes in the Uterus during Sexual Cycle.—During procœstrum there is injection and swelling of the mucous membrane of the uterus, followed by capillary hæmorrhage, extravasation of blood, and later, in the human subject, destruction of the mucosa and epithelium. In the woman, hæmorrhage occurs into the interior of the uterus, and the uterine glands pour out their secretion; in due course the mucosa and epithelium are repaired and the hæmorrhage ceases. In the herbivora there is no destruction of the mucosa, and but slight destruction of the epithelial layer; capillary hæmorrhage of the cotyledons occurs in ruminants, but of a limited character; the mucous glands of the uterus and vagina pour out a secretion, and it is this, together with the capillary hæmorrhage, which gives rise to the slight discharge observable. In sheep of more than a year old the mucous membrane of the uterus during the period of 'rest' may be observed to be black with pigment, the result of extravasated blood. In carnivora more extensive changes occur than in herbivora, but not nearly so destructive as those taking place in women and the monkey.

As a result of these changes the uterus is prepared for the arrival of a fecundated ovum, procœstrum passes away, and is followed by œstrus.

Rutting.—When male animals suffer from a periodic sexual excitement, it is known as rutting. This term should be confined entirely to a male sexual season, such as is experienced by the camel, stag, elephant, and ostrich. In the rutting stag the neck becomes enormously swollen (Leeney), the elephant experiences a discharge from the temporal gland, the camel eats little, and in consequence becomes 'tucked up'; he also protrudes from the mouth a disgusting-looking bladder formed by the soft palate; the ostrich becomes red in the legs. All these animals are at this time dangerous to approach, being invariably violent and aggressive.

During the period of ' rut ' mature spermatozoa are produced, and probably at no other time. In insectivora and rodents there is a growth of the generative organs, especially the testes, which, if intra-abdominal, may shift position, and appear externally. In the hedgehog the seminal vesicles and prostate gland assume remarkable proportions, shrinking to normal when the period of excitement has passed away; in the mole the testicles become sixty-four times larger than during the resting period; the preputial glands of many animals emit a penetrating odour of musk. ' Rutting ' is due to an internal secretion of the testicle elaborated by the interstitial cells.

A male generative cycle does not occur in domesticated animals. Nevertheless, both the dog and cat give evidence of what might be regarded as ' rutting ' when aware of the existence of an œstrous female.

Desire in all male animals is due to a hormone produced by the interstitial cells of the testicle (Leydig's). These cells are also present in the epididymis, and account for the sexual characteristics present in animals in which the epididymis has not been removed in the operation of castration. They are likewise the cause of the desire met with in animals in which the testicles have not descended, though such cases are frequently sterile owing to the absence of spermatozoa. If the testicles be exposed to X rays the spermatic cells are destroyed, but not the interstitial cells of Leydig. The animal consequently does not lose desire, but is rendered sterile.

The Cell.—It will help to a clearer understanding of the structure and development of the ovum if the features of body cells in general are considered.

There are two distinct classes of cell in the body. The more numerous tissue cells, known as *somatic* or *body cells*, are responsible for the structure of every tissue in the body, from the hardest to the softest. Another and much smaller set are the *germ cells*, which are concerned solely in the reproduction of the individual. The somatic cells are enormously active during embryonic life, and subsequently during the process of growth. When this is completed, they settle down to normal activity, which consists in growth by the process of division; by this process of multiplying they are capable of repairing or replacing the worn-out cells of the body. The living animal is merely a gigantic collection of cells, each having an individual existence. As the cells die or are worn out, their places are taken by others, and this process is occurring during the whole life of the animal. Within this minute speck of material is contained all the elements of life, and, small as it is, it contains all that is necessary for multiplying and producing its kind, in this respect differing in no essential particular from the larger organism of which it is only a microscopic atom.

All cells, somatic or germ, consist of cell-contents and cell-wall. The contents are colloidal in character, structureless, and are generally described as *protoplasm* or *cytoplasm*. Within the cell and lying in the cytoplasm is the *nucleus*. The nucleus consists of nuclear membrane and contents, but the latter are not structureless. The nucleus of all cells is an important feature, without which the cell could not be reproduced. The reproductive material

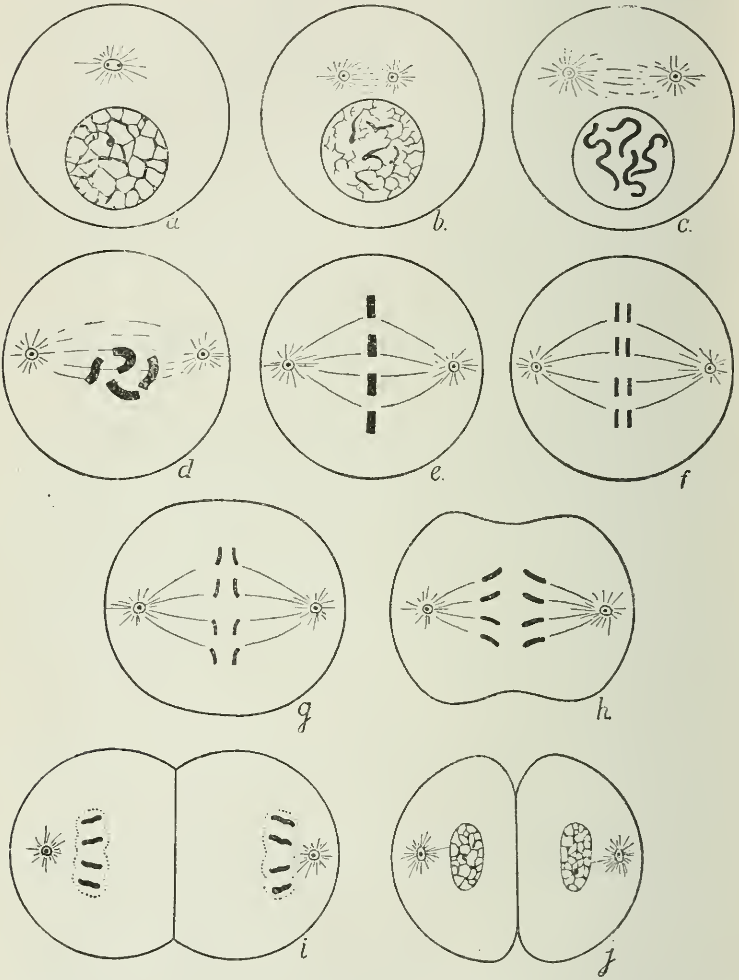

FIG. 258.—DIAGRAM ILLUSTRATING THE PROCESS OF CELL DIVISION (AFTER BOVERI).

in the nucleus consists of a network of threads (Fig. 258, *a*), which, owing to their affinity for staining material, are known as *chromatin*. Within the threads are refractile bodies. In addition to the nucleus, the parent cell contains a spherical area of protoplasm, known as the *centrosome*, a body of the utmost importance. The centrosome is surrounded by radiating fibrils, which give it the appearance of a star (Fig. 258, *a*), and the area surrounding it is spoken of as the *attraction sphere*. The reproduction of cells is brought about by indirect division, or *mitosis*, and the change is initiated in the nucleus, or in the case of the centrosome by division of the body. The chromatin threads of which the nucleus consists form larger threads by the process of fusion until the network is lost, and there only remains a collection of bodies resembling bent or curved rods (Fig. 258, *b*, *c*). These are the *chromosomes*, and the number present in each cell of the body is always definite for the particular species, but is not the same in all species of animals. There are, for example, twenty-four chromosomes in the mature somatic cells of man, the mouse, trout, salamander, and lily; in some of the threadworms there are two; in some of the crustacea as many as 168. The number of chromosomes in the horse is thirty-six plus one *accessory*; in the mule fifty plus one accessory; in the ass there are probably sixty-five;* in the cow sixteen. No matter what somatic cell is examined, the number is invariable for any given animal. The importance attached to the number, which is always even for every animal and plant sexually produced, will shortly be evident. The chromosomes themselves are of extraordinary interest.

The first change preparatory to the division of any cell takes place, as has been stated, in the nucleus, and while this is occurring the centrosome has divided into two, passing to opposite sides of the nucleus (Fig. 258, *b*, *c*, *d*); these, with their star-like fibrils, are known as *astrospheres*. The chromosomes being formed, the cell wall of the nucleus disappears, and so liberates them (Fig. 258 *d*); they are then arranged between the two poles formed by the astrospheres, placing themselves end to end in Indian file equatorially (Fig. 258, *e*), and, having done this, they split longitudinally, and each forms two (Fig. 258, *f*). Each split chromosome is attracted towards the astrosphere nearest to it, so that an equal number of chromosomes pass to each of these bodies. The cytoplasm of the cell has hitherto been an inactive witness of this remarkable phenomenon. It now, however, divides into two portions (Fig. 258, *h*, *i*, *j*), each engulfing an astrosphere with its attendant chromosomes, and in this way two cells are made out of one, which resemble the parent in every respect, excepting that they contain only half the amount of chromatin, though the full number of chromosomes is present. The subsequent history of the new cell is simple. The chromosomes come together, form a reticulum, surround themselves with a membrane constituting the cell wall of the nucleus, and increase the amount of chromatin up to that originally existing in the parent cell (Fig. 258, *j*). Every body cell contains, therefore, a double set of chromosomes; each time a cell divides half of the chromosomes pass to the new cell, and in course of time the divided cells again form a double set.

Every animal originates from a cell which differs in no essential particulars from the one just described. The process of multiplication by which cells form a lion or a mouse, an elephant or mole, a philosopher or an idiot, or a humble intestinal worm, are in all cases identical. In the development of the ovum the stages through which the higher animals pass before they become higher may, as it were, be witnessed or readily visualised. There is nothing in the early development of the ovum which sharply defines man formation from dog, cat, or pig formation; each goes through the same phases up to a certain point, and then comes the parting of the ways. The unity of type of the embryo in its early stages is succeeded by sharp differentiation; this is even more remarkable than the incomprehensible likeness of the starting-points.

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* 'Causes of Sterility in the Mule,' J. E. Wodsedalek, *Biological Bulletin*, vol. xxx., 1916. The accessory chromosome referred to in the text is explained at p. 781.

How does a cell work? It respires in the sense that it takes up oxygen and gives up carbon dioxide. It feeds, for the particles of food in the amœba may be seen passing into the interior, where they are digested. No rupture of the cell wall occurs in consequence of this ingestion of food material; the substances pass through and the gap closes behind them. The cell moves, for the movements may be seen; those connected with the white blood-corpuscles and amœba have been described and figured at p. 16. The movements are effected by protrusion of protoplasm, the cell wall being pushed out as the result of change either of the fluid pressure within the cell or of the fluid medium in which all body cells are bathed.

The cell wall is permeable to certain solutions, but not to others. The conception of the cell wall is that it is finely perforated and permits the passage of molecules which are small enough to pass through, those too large being held back. This passage through a cell wall is produced by differences of molecular concentration known as osmosis, to which subject reference has been made at pp. 277, 278. At p. 279 will be found a reference to the influence of electrolytic action in living cells, a subject intimately concerned with that of osmosis.

It has been mentioned above that the cell cannot be reproduced without a nucleus. At p. 471 evidence of this fact has been adduced.

It is impossible in a work of this kind to enter more deeply into the physiology of the cell. It is obvious that a knowledge of the cell is intimately connected with the nature of life. All the physiological processes of the body which have been considered in previous chapters are carried out by the cells, and the methods by which they work are chemical, physical, and biological problems of great complexity, which, if fully understood, would explain the enigma of life.

Maturation of the Ovum.—The maturation of the ovum is not the same as its fertilisation. Maturation is concerned with the production of a perfect from an immature ovum, of a mature from an embryonic cell. This process is effected on the lines above indicated. It has been stated that the cells in the ovary at birth are imperfect; their number is laid down, and this we have seen amounts to several thousands. They are completed as required, and are only matured some months or years after birth, depending on the species of animal. It is obvious that only a few are matured at one time, and, again, the species of animal determines whether they are matured, as in the woman, at short regular intervals, or at relatively long intervals. The periodical development of a mature egg or eggs constitutes the essential feature of maturation.

The primitive ovum takes its first step towards maturation by the process of cell division. Two cells unequal in size result: one is the ovum, the other the *first polar body*. The number of chromosomes in the immature ovum was originally, in the case of the mare, thirty-six; as the result of the formation of the first polar body, these thirty-six fuse and form eighteen. Before the first polar body is cut adrift the eighteen chromosomes split, so that eighteen go to the polar body and eighteen remain with the ovum. Though these two cells contain only half the number of chromosomes contained by a somatic cell, yet each is a whole chromosome, and not a half, as in the division of somatic cells. The ovum now divides a second time, and extrudes a *second polar body*. This time the eighteen chromosomes either split or divide, thus forming thirty-six; half pass to the second polar body, and half remain with the parent cell, the ovum. So that the formation of the two polar bodies has caused the ovum to suffer a loss in the number of chromosomes, and it is finally left with only half its original number; but its cytoplasm has undergone no practical loss. The polar bodies are regarded as abortive ova; they die, and are not concerned in the subsequent changes. The important point is that the mature ovum is left with only half the number of chromosomes normal to the cells of the species. One further change in the process of maturation has also taken place, and that is the centrosome of the cell is lost. These remarkable changes pave the way to an understanding of what follows, should impregnation of the ovum occur.

An ovum without a centrosome and with only half the normal number of chromosomes has, in order to be fertilised, to be furnished with a centrosome and its full number of chromosomes. It is the function of the spermatozoon to supply these (see p. 740). It is evident that the two sets of chromosomes described at p. 753 as existing in the body cells of animals are derived from its parents, one set from the sire and one set from the dam. The chromosomes are believed to convey the hereditary characters of the transmitters, but there are arguments to the contrary (see, however, p. 799).

Ovulation.—This occurs at the moment the Graafian vesicle ruptures and the ovum is ejected. In some animals. as the rabbit and ferret, it can occur only as the result of coition, the presence of spermatozoa in the uterus being essential to the act. In others—and they represent the majority—such as the mare, ass, cow, sheep, pig, and dog, ovulation occurs during œstrus—

in the case of the mare, frequently towards the end of the œstrus period (Ewart)—so that the act of copulation is not necessary to extrusion, and in such animals artificial insemination is therefore possible. The period of œstrus is not necessarily identical with the period of ovulation; œstrus may occur without ovulation, and ovulation may occur without œstrus. Ewart says the mare may mature and discharge one or more eggs after she has become impregnated; this is known to occur in other animals, including man, and accounts for **superfœtation,** or the production of a second conception in an animal already pregnant (see p. 783). The number of ova which may be extruded during one sexual period is not known with any degree of certainty; in the case of the cat and dog there is evidence of several being ejected, for each fœtus represents a separate egg; the number of eggs extruded in such cases is in excess of the number impregnated. The mare, which probably produces only one egg at a time, and with whom twin births are very rare, is believed by Ewart to shed about ten or twenty ova annually. Whether an equal number is discharged by each ovary is unknown. Probably one ovum for the mare, cow, ass, deer, elephant, or monkey, at each œstrus period is the rule, though two may be discharged. The sheep probably discharges one to four; the dog, wolf, and cat five to six; the pig ten, or even fifteen. The egg or eggs, having been extruded, find their way into the Fallopian tubes in a manner already described (p. 744).

The **Period of Puberty,** or the age at which an animal becomes capable of procreation, has been put at one and a half years for the horse, eight to twelve months for bovines, and six to eight months for the sheep, pig, and dog. The full development of the reproductive system is greatly influenced by the question of nutrition, well-fed animals arriving at puberty earlier than those which have been underfed. There is, however, a great difference between capability and *fitness* for procreation.

The advent of puberty is marked by the production of the secondary sexual characters. The animals lose their awkwardness, the outline of the frame becomes more consolidated and in greater unison. The organs of generation are in a state of activity. In the male the neck becomes thick and curved, the voice deepens, and the whole appearance denotes life and vigour. In both the stallion and bull the temper is usually irritable and uncertain, and often extremely vicious. These changes occur gradually, and are fully established at **maturity.** In the horse maturity is commonly believed to be attained at five years of age; it is probably attained nearer six, and some have thought even later than this. The ass, according to Crisp, is mature at five years old; the ox, sheep, and goat at four; the pig at three.

The age at which procreation ceases is not known. Mares have produced foals at twenty-eight, thirty-two, and thirty-eight years of age,* and it is certain that some good stallions have been advanced in years. There is not present in the horse, ruminant, or carnivora any 'change in life' such as women, and men in a less marked degree, experience as the result of age.

The **Act of Erection** is a vascular phenomenon produced by an engorgement of the erectile tissue of the penis with blood. This engorgement is brought about by stimulation of the *nervi erigentes*, which are derived from the autonomic system, and arise from the sacral portion of the cord. These nerves furnish dilator fibres to the vessels of the penis, and under their influence the cavernous spaces of the erectile tissue become gorged with blood under pressure. The *nervi erigentes* act reflexly through an erection centre in the cord, while the erection centre is under the influence of higher centres in the brain. Erection and ejaculation in the dog may be produced by stimulation of a definite area of the cortex of the cerebrum; they may also be produced without the knowledge of the animal—for example, after section of the spinal cord in the lumbar region. The sensory nerves in the penis, by which erotic sensations are carried, are the pudic; if the pudic nerve be cut erection is impossible; if the central cut end be stimulated it leads to ejaculation.

The first portion of the penis which receives the excess of blood in erection is the *corpus cavernosum*; the spongiosum and glans are not fully erect in the **stallion** until the penis is within the vagina. The *erector penis* muscle compresses the penis against the pelvis, and by thus blocking the return of blood assists in maintaining erection. Before ejaculation in this animal the glans swells enormously, resembling the mouth of a trumpet, apparently in order to cover or grasp the os uteri. After intercourse the organ is withdrawn into its sheath by the contraction of a pair of unstriated muscles, known as the *retractor penis*. Though the organ in the horse assumes such considerable proportions, in the **bull** this is not so. The peculiar penis in this animal undergoes very little vascular engorgement; it is already firm (see p. 737). In the act of erection the retractor penis muscle is inhibited, and the **S**-shaped curve of the penis removed; by this means the organ gains considerably in length. At the same time the retractor muscles of the sheath draw back the prepuce. In the **ram,** erection and elongation are carried out as in the bull, the vermiform appendix (see p. 737) undergoing peculiar gyrations before penetration. It is believed by many that the vermiform appendix is essential for successful impregnation, for if it be removed, it is said, the animal proves sterile; this is certainly not invariable.* In the **dog** the increase in the size of the penis is mainly at its posterior part, at the bulbous swelling there observable, the bone in the penis of this animal facilitating its introduction into the vagina.

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* In a paper on 'The Growth and Maturity of Animals,' by Dr. E. Crisp, referred to above, the writer states he knew a Suffolk cart-mare that bred a foal at the age of thirty-nine (*Veterinary Review and Stockowners' Journal*, March, 1865). The 'Tartar Mare' was considered to be thirty-four to thirty-six years of age when she bred 'Queen Mab.' 'Driver,' an Australian imported mare, bred 'Moss Rose' at thirty-three (*Standard*, December 25, 1893).

Mr. F. T. Harvey, F.R.C.V.S., informs the writer that he has known a cow breed long after the loss of all her incisors as the result of age.

Sexual Intercourse.—Copulation is not necessary in all animals, nor indeed in any. What is required is merely an interchange of elements from the nuclei of two different kinds of cells. To this last statement a slight exception might be taken, because there is a condition—*parthenogenesis*—where the access of a second element is not required, but this method of development is unknown in the higher animals. The act of intercourse is of short duration in the majority of animals, excepting the dog and pig. The friction of the male organ leads to ejaculation, a process confined to the male.

In a vigorous stallion the period of intercourse is from five to ten seconds; when exhausted, from fifteen to twenty seconds. For the bull and ram intercourse is very brief—one to two seconds. In the pig and dog it is prolonged, the boar occupying about ten minutes. In the case of the dog the actual period of excitement to ejaculation is brief—about four seconds—but sixteen or seventeen minutes may elapse before the sexes are parted, owing to the incarceration of the bulbous swelling by contraction of the sphincter muscle of the vagina. The object of this will be explained presently.

During coitus the clitoris of the female is erect and the sphincter vagina muscle stimulated to contraction; the vessels of the vulva are dilated, and the uterus is believed to become erect and undergo a series of peristaltic contractions, the os dipping down into the pool of seminal fluid and probably sucking it in by aspiration. These movements have actually been observed in the rabbit. The glands of the vaginal canal also pour out a secretion.

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* Mr. Hugh Begg, F.R.C.V.S., has been good enough to make inquiries for me on this point from breeders and others. Mr. M. G. Hamilton, of Cobbinshaw, Lanarkshire, informs him that a famous black-faced ram, 'Radium,' lost the entire appendix through sloughing, owing to an operation for the relief of an impacted calculus. This animal, when there was 'not a vestige' of the appendix left, was a sure stock-getter for the next five years, and three of his sons took prizes at the Highland and Agriculture Show at Aberdeen in 1908. Mr. Hamilton adds that since then he has used another ram without the appendix with equally good results, and knows of other stockmen with similar experience.

Mr. P. Wilson, M.R.C.V.S., of Lanark, says he has removed the appendix, and the animals have subsequently been successfully used for stud purposes.

Ejaculation is a complex reflex act in which the seminal tubes of the testicle, the epididymis, vas deferens, and accessory glands are all stimulated by a definite series of muscular contractions to press out their contents, the bulbo-cavernosus and ischio-cavernosus muscles by rhythmical contractions forcing the fluid along the urethral canal. This act is accompanied by up and down movements of the tail in the horse and by alternating movements of the hind-feet in the dog. It is only recently that anything like precise information of the details of ejaculation has been obtained through the researches of E. Iwanow,* whose work we will now follow.

In the horse the semen is ejaculated by an intermittent jet; the first portion consists of a little clear fluid from the urethral glands, which it is thought is intended for the purpose of washing out and disinfecting the urethra (see p. 742); the next secretion is that produced by the glands of Cowper; then follows the true seminal fluid, which is diluted in the prostatic portion of the urethra by the secretion of the prostate (see p. 742); and, finally, a rather gelatinous and thickish mass of material, believed to be derived from the vesiculæ seminales, and containing few, if any, spermatozoa (p. 742).

An emission in the horse is from 50 to 100 c.c. (1·75 to 3·5 ounces), though Iwanow states he has measured emissions of 300 c.c.

In the bull the amount ejaculated is about 100 c.c. (3·5 ounces), and in the ram from 2 to 5 c.c. (34 to 84 minims). Iwanow gives very detailed information in respect of the dog. In this animal there are three stages of ejaculation. The first lasts from 6 to 26 seconds, followed by an interval of from 8 to 26 seconds; then succeeds the second ejaculation, which lasts 10 to 44 seconds; this is followed by a third ejaculation, which occupies from 4 to 16 minutes or longer. The amount of fluid ejaculated at the first and second evacuation is in each case from 1 to 2 c.c. (17 to 34 minims); the third ejaculation is much larger, and amounts to 10, 15, 20, or even 29 c.c. (0·35, 0·5, 0·7 to 1 ounce).

This amount of fluid, which obviously must vary depending upon the size of the animal, is largely due to the activity of the prostate; the other accessory glands take very little share, and there are no vesiculæ in the dog; nor is the seminal fluid derived directly from the testicle, but from the reserves in the epididymis and the ampullæ of the vas deferens. Hitherto it has been impossible to explain why the canine species should be locked together; we now know that it is due to the prolonged character of the ejaculatory reflex.

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* *Op. cit.*

Probably in no animal is the whole of the seminal fluid retained. In the case of the mare there are expulsive efforts, apparently not under the control of the will, though every effort is made to prevent them occurring. As far back as the seventeenth century the method was to give a gallop immediately the stallion had descended; the Arabs and other nations have employed water thrown on the hind-quarters of the mare. It is quite clear that with such a large ejaculation as the stallion possesses there must be an outflow of fluid, the greater part of which, as we have seen, is sterile. In the case of the cow there is a slight loss, but not invariably so. What occurs at the height of the orgasm is by no means clear. The stallion has a projecting urethra and a trumpet-shaped glans which is quite capable of embracing the os, while the projecting urethra enters it or is applied closely to it. Whether some sperm is actually injected into the uterus, as we believe, can only be settled by experimental inquiry. The bull, ram, and boar are also provided with means of effecting a direct entry into the uterus. The vermiform appendix of the ram may actually enter the os, but at present nothing definite is known. In the case of the dog the penile bone and the prolonged period of vascular engorgement are eminently favourable for the passage of fluid into the uterus, but again the point is not clearly known. In both the dog and rabbit spermatozoa have been found in the uterus immediately after coition, which is suggestive of direct entry. In all animals the aspiratory action of the uterus must also be taken into account in deciding this question. Artificial insemination, now so widely practised, depends very largely for its success on the introduction of the seminal fluid *into* the uterine cavity. It is well known, however, that in intercourse conception has followed when the semen has penetrated no farther than the inside of the vulva. As we have already seen, spermatozoa may remain alive for many hours outside the body if kept under suitable conditions of warmth and darkness (see p. 741); while in the passages of the female the precise limit of their vitality is unknown; a fortnight is probably the maximum period. F. B. Sumner* is of opinion that in the case of mice the spermatozoa may remain alive for weeks after their reception into the uterus or Fallopian tube, and it is known that in the bat they may remain alive for some months after coitus.

* *Biological Bulletin* (U.S.A.), vol. xxx.

Fertilisation.—The activity of the spermatozoa is the means by which fertilisation is effected; they swim or move by a wave-like motion of the tail; the head remains motionless. Iwanow tells us that there are 841 millions in the seminal evacuation of the dog, but as only one is required for a single ovum there is an enormous waste of fertilising material, and this occurs both in animals and plants. The vast majority of the sperms must therefore die, and the seat of their disintegration must be throughout the length of the uterine horns and Fallopian tubes. Guided by some extraordinary instinct, if the term may be employed, the spermatozoa have only one objective, and that is to reach the Fallopian tubes. The presence of cilia in these offers no obstacle, though they create a current in the opposite direction to that in which the spermatozoa are travelling; in fact, it is said that an opposition current renders their movements more vigorous. In due course they reach the tubes, and in the case of the rabbit have been found at the upper end of the Fallopian tube nine or ten hours after coition. The periods in other animals are unknown; they are probably variable, but under no circumstances would it appear to be longer than a day or two.

Fertilisation of the Ovum.—Somewhere in the Fallopian tube, though occasionally on the surface of the ovary, the meeting between the sperm and germ cell occurs; what is known of the mechanism of the passage of the ovum from ovary to Fallopian tube is described at p. 744. Owing to the enormous number of sperm cells existing even in a droplet of the secretion, it is easy to understand why the ovum cannot escape coming in contact with them. A single spermatozoon penetrates the wall of the ovum, and enters the cytoplasm. Others may attempt to follow, but the surface of the egg at once becomes impervious to further attacks. The spermatozoon, having got inside the egg, loses its tail, which is no longer required. The essential portions of the organism are the head and middle piece. The former is the cell with its nucleus, which contains the all-important chromosomes; the middle piece contains the centrosome, which, it will be remembered, was lost to the mature ovum. There are now two nuclei within the egg—one the male, the other the female *pronucleus*. These meet, fuse, and, under the direction of the centrosome, the process of cell division immediately follows. The union of these two nuclei is a matter of extraordinary importance. It will be remembered that by a process of reduction the chromosomes in the ovum and spermatozoon were reduced in each case to one-half. As the result of the union of the nuclei, a *segmentation nucleus* is formed. From this segmentation nucleus the future animal is formed. The segmentation nucleus divides, the chromosomes it contains *split*, so that each division of it contains the number of chromosomes normal to the species, the essential feature being that each parent is represented in each division of the cell and in all subsequent subdivisions. It necessarily follows that not only are the parents represented, but in a less degree the ancestors on both sides (see p. 799).

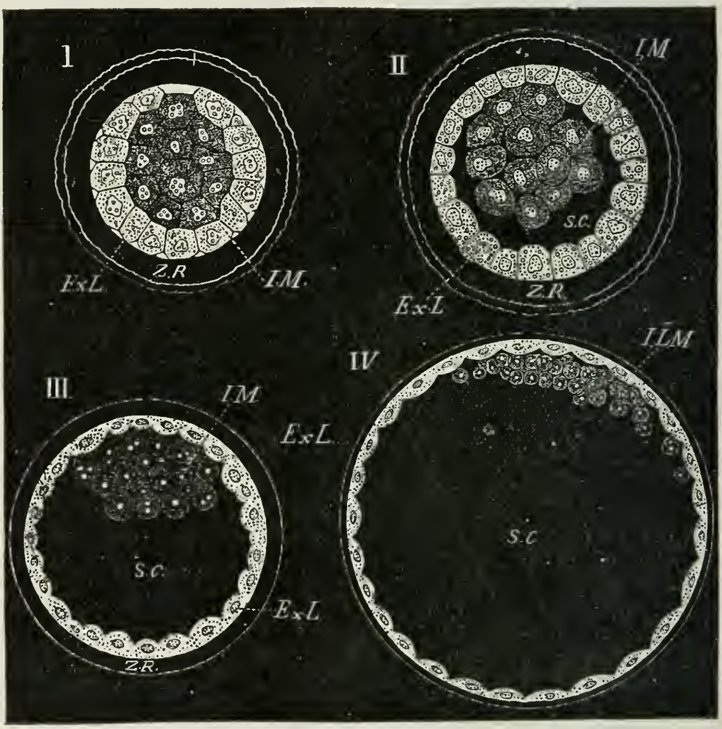

Fig. 259.—Section of a Rabbit's Ovum at the Close of Segmentation. II., III., IV., Stages in the Formation of the Blastodermic Vesicle (E. von Beneden).

Z.R., Zona radiata; *Ex.L.*, external layer of cells; *I.M.*, inner mass of cells; *I.L.M.*, inner lenticular mass of cells; *s.c.*, segmentation cavity.

It will be observed that the spermatozoon and ovum are the complements of each other. The ovum contains an abundance of cytoplasm and a nucleus, but no centrosome; the spermatozoon contains no cytoplasm, but both a nucleus and a centrosome; the characteristic common to the two is that they both contain the same number of chromosomes. There is a great deal of experimental work which tends to show that if to the ovum a centrosome be supplied, or if to the spermatozoon some cytoplasm be given, development will occur without the aid of spermatozoon or ovum.* Loeb has shown that by physicochemical means the eggs of the sea-urchin may be made to develop into larvæ, though normally a spermatozoon is required for this purpose.

When segmentation of the ovum is completed, as indicated in Fig. 259, I., a sphere is formed (Fig. 259, IV.), consisting of an outer cellular layer, formed of single cells (*Ex.L.*) enclosing a cavity known as the *segmentation cavity* (*s.c.*). The sphere is called the *blastodermic vesicle*. It contains broken-down yolk, and at one part some smaller cells (*I.L.M.*), which probably spread over the inner wall of the sphere and form an inner cellular layer. The outer cellular layer (*Ex.L.*) is the *epiblast*; the inner cellular layer (*I.M.*, II.) is the *hypoblast*. While the latter is spreading

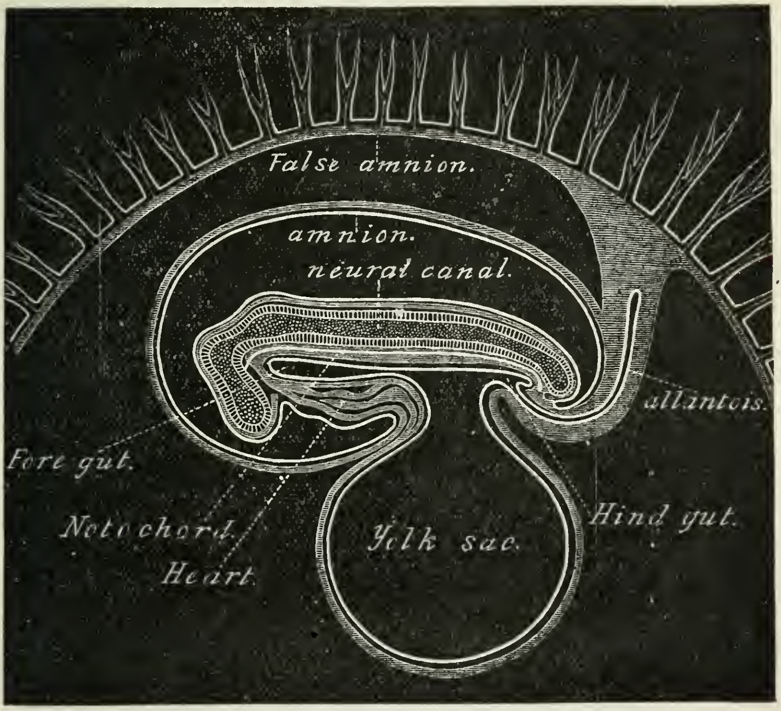

FIG. 260.—DIAGRAM OF A LONGITUDINAL SECTION OF A MAMMALIAN OVUM AFTER THE COMPLETION OF THE AMNION (SHARPEY-SCHAFER).

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* There are some eggs which normally develop without the intervention of the male element; this is known as *parthogenesis*.

over the inner wall, a white disc is developed at one point of the vesicle; this disc is the *germinal area*. In this area the embryo develops. A development of the cells of the epiblast leads to the formation of a groove in the area, known as the *primitive groove*; the sides of the groove grow up, meet, and enclose a space—the *neural arch*—and from this arises the cerebro-spinal system. A third layer of cells now develops between the epiblast and hypoblast, and is spoken of as the *mesoblast*.

The mesoblast furnishes a layer of cells under the neural canal, the *notochord* (Fig. 260); from these the bodies of the vertebræ develop. The mesoblast splits: the outer layer of it unites with the epiblast, and so forms the *somatopleure*; the inner unites with the hypoblast, and forms the *splanchnopleure*. As the result of the splitting, a cavity is formed between the layers, known as the *pleuro-peritoneal space*, or *cœlom*. This is the body cavity of the future embryo. From the three layers of cells developed around the ovum the following tissues of the embryo are formed:

From the Epiblast:

- The whole of the nervous system, both cerebro-spinal and sympathetic.
- The epithelial sensory end-organs of the nerves of special sense, and the crystalline lens.
- The epidermis and its appendages—hair, hoof, claws, horns.
- The epithelium of all glands opening on the surface of the skin, including mammary, sweat, and sebaceous.
- The epithelium of the mouth (not the tongue) and glands opening into it, the enamel of the teeth, and the epithelium of the anus.
- The epithelium of the nasal passages and facial sinuses.

From the Mesoblast:

- The bones, cartilages, and connective tissues of the entire body.
- The whole of the muscles, skeletal and visceral.
- The entire vascular and lymphatic system—blood-corpuscles, spleen, and serous membranes.
- The generative organs and generative elements.
- The urinary organs.

From the Hypoblast:

- The epithelium of the alimentary canal and the ducts of all glands opening into it.
- The epithelium of the respiratory organs.
- The cells of the liver and pancreas.
- The epithelium of the bladder, ureters, thyroid body, and part of thymus gland.

During the growth of the mesoblast the embryo, which is developing in the germinal area, is gradually being lifted off the blastodermic vesicle by the formation of a sulcus or depression which extends around it. The embryo at this period possesses within it two tubes—one dorsal (the neural canal), the other ventral (the alimentary canal). The latter opens in front and communicates with the yolk sac (Fig. 260), the earliest source of nourishment to the embryo.

It is not our intention to carry the development of the ovum beyond the above point. It is, however, most essential to understand in what way the ovum behaves on entering the uterus, how it is nourished before and after the circulation is established, and the nature and function of the various membranes within which it is contained.

Implantation of the Ovum.—At every monthly period in the human female the mucous lining of the uterus undergoes certain changes, which result in the formation of a membrane known as the *decidua*; this is in shape a counterpart of the interior of the uterus. The membrane is shed during menstruation; if the woman becomes pregnant the decidua is not exfoliated, but undergoes further development in connection with the ovum. The latter on its arrival in the uterus becomes *embedded* in the folds of the mucous membrane, which grow up around and anchors it to the wall of the uterus. That portion of the mucous membrane which grows over and envelopes the ovum is known as the *decidua reflexa,* that which lines the interior of the uterus is known as the *decidua vera.*

In that portion of the human decidua between the ovum and the uterine wall known as the *decidua reflexa* or *basalis* is formed the *placenta,* a cake-like mass of vascular tissue in which the interchange of blood between the mother and fœtus occurs. The placenta normally forms at the upper part of the body of the uterus, so that the ovum hangs from the roof. The reflexa lying between the ovum and uterus consists of two layers: that nearest the ovum is a compact layer, that next the uterus is a spongy layer, the spongy appearance being due to the dilated uterine glands. From the surface of the ovum, processes (chorionic villi) grow into the compact layer and then into the spongy layer, where in due course they meet with the maternal blood, in which *they are bathed.* The villi accordingly bring about tissue destruction, either by phagocytosis or enzymic action, and this erosion is effected by a special layer of cells belonging to the embryo known as the *trophoblast.* The function of the trophoblast in all animals is to effect connection between the mother and the embryo.

While this connection is being effected the embryo is growing and being nourished by means which need not detain us; blood is being formed in it which leaves the body in a structure known as the *connecting stalk*; it is the growth of these vessels (villi) through the layer of the decidua basalis into the excavated blood-sinuses in the uterus of the mother, which culminate in the placenta.

The Placenta.—We need not follow the formation of the human placenta any further, but what has been said will enable the arrangement in animals to be better understood.

No domesticated animal, with the exception of the dog and cat, has anything resembling a decidua, and even in these the resulting placenta is quite different from that of man. Consequently, a primary classification of animals has been into *deciduate* and *indeciduate*, but these terms are no longer retained for morphological purposes, as the chief interest is centred, not in the decidua, but in the group of cells described above as trophoblastic, the function of which in all placental mammals is to establish a nutrient connection between the embryo and the parent. This group of cells belongs to the embryo. Where there is a decidua they work as above described; where there is no decidua they work direct into the various pits and crypts in the mucous membrane of the uterus, but do not destroy the mucous membrane; therefore they do not create blood-sinuses in the walls of the uterus, and the fœtal villi are *not bathed* in maternal blood, but merely brought sufficiently close to the vessels of the mother to obtain the necessary exchange of blood, gases, and nutriment.

If this sketch of deciduous and indeciduous mammals is understood, the first step is taken towards the comprehension of a very complex subject, many of the details of which still await settlement. One further point in the comparison must, however, be mentioned. In man the blood which finds its way into the chorionic villi of the embryo and establishes the placenta is carried by the ' connecting stalk '; whereas in all domesticated animals the placenta is vascularised by the allantoic sac, a large and important structure, which in man is of extreme insignificance.

Even the deciduate dog and cat have the placenta vascularised from the allantois.

Types of Placenta.—It is convenient here to draw attention to the appearance presented by the placenta in various animals. In man it is a circular, flat cake, about 6 inches in diameter and 1 inch in thickness, located in the body of the uterus as far away from the internal os as possible. The reason is obvious; if near the os, the placental connection with the child is destroyed in the early stages of labour, and, further, the woman frequently bleeds to death. This condition is known as *placenta prævia*, and is impossible in the domesticated animals other than the cow, in which a cotyledon has been known to lie near the os.

In the dog and cat the placenta consists of straps or bands of villi surrounding the elongated ovum, the straps being placed well apart. This is a *zonary placenta*.

In the ox and sheep the placenta consists of sixty or more vascular knobs (*cotyledons*) scattered over the enveloping membrane of the fœtus, and directly attached to a similar number of cotyledons on the mucous membrane of the uterus of the mother. This is a *cotyledonary* or *multiple placenta*.

In the horse and pig the placenta consists of one large vascular sheet completely encircling the fœtus, and consequently intimately in contact with the mucous membrane of the entire uterine horn or horns in which development occurs. This is known as a *diffuse placenta*, and is the most primitive variety known.

The vascular or semi-vascular membrane of the above types, the villi of which, by union with the uterine wall, form the placenta, is known as the *chorion*.

Nutrition of the Embryo.—The fertilised egg does not pass rapidly through the Fallopian tubes to the uterus. In the *sheep* the period occupied is four to five days; no definite periods have been fixed for the other domesticated animals, but the time is known to be comparatively long in the dog and cat. Probably in all the ovum has reached the uterus in the course of eight days. In the tube it is still surrounded by the zona pellucida (p. 744) and a sticky gelatinous layer (the *prochorion*). The latter furnishes nutriment until better arrangements can be made. On its arrival in the uterus the bloodvessels and lymphatics of this organ dilate, the mucous membranes become œdematous, and a glandular secretion is poured out for the purpose of nutrition. The egg is not at once fixed to the wall of the uterus in domesticated animals; it has a period of freedom which varies in the different species. In the *sheep*, for instance, it is free until the seventeenth day, and its attachment to the mucosa is completed by the thirtieth day (Assheton). During this time, however, the development of the ovum is not delayed. The prochorion ruptures at the ninth day; the trophoblast is formed, and eventually comes into contact with the wall of the uterus; the germinal vesicle elongates and fills the uterine horn, or both horns if only one embryo is present (Marshall). The yolk sac (yet to be described) is formed, and the allantois takes shape and grows rapidly, furnishing the blood which forms the villi seen on the twenty-eighth day on the external covering of the embryo. These villi fit into crypts in the cotyledons. By the forty-fourth day the fœtal cotyledons are scattered over the whole surface of the embryonic covering, and by the seventy-eighth day the general character of the placenta is established (Assheton). In the *pig* the impregnated ova are spherical until the tenth day; then they elongate, and by the tenth day fill the horns of the uterus, which is contracted between each ovum. In the *mare* no details are known of the early behaviour of the ovum; according to Ewart, it is usually located in the right horn. For the nutrition of the horse embryo from the fourth to the ninth week see p. 775, where it is inserted as a matter of convenience in considering the question of the death of the embryo. In the *dog* and *cat*, owing to the thickness of the gelatinous layer (prochorion) the ovum does not become adherent to the uterus until the twentieth day in the dog, and the twelfth day in the cat. No matter what delay occurs in attachment, the development of the ovum continues to progress, its nutrition being furnished by the fluid found in the uterus, and presently by the trophoblast and yolk sac.

The *trophoblast*, a layer of cells of extraordinary importance, is formed on the outer enveloping membrane of the ovum; its function, as previously indicated (p. 766), is to form a vascular connection with the uterine wall, and so furnish nutriment to the developing egg. It takes no part whatever in the formation of the embryo or its membranes. In animals possessing no decidua (herbivora, etc.) it first becomes adherent to, and then eats its way into, the mucosa, probably by phagocytosis. The epithelium and glandular structure are reduced to a débris, and on this the trophoblast lives, ingesting the blood-cells and leucocytes. In cotyledonary placentæ it also attacks these enlargements; there being no glandular substance within them, their destruction is less; but there occurs effusion of blood, which the trophoblast utilises, while at the same time it is preparing the cotyledons for the reception of the villi which are presently pushed out, and gain attachment to them. Not only does the trophoblast take up broken-down tissue cells and liberated blood-cells, but also *uterine milk* furnished by the glands of the uterus, and this in ruminants is the most important source of nourishment taken up by the trophoblast. In the deciduata (carnivora), as in the indeciduata, the mucous membrane of the uterus is previously prepared for the ovum; the epithelium is swollen, the glands and crypts enlarged, the spongy and compact layers (p. 765) are formed in the region where the trophoblast will unite. The trophoblast, followed by villi pushed out by the developing embryo penetrates to the capillary layer of the uterus leading to a disappearance of the maternal tissues less the capillary vessels which are left as a skeleton, into and between which the villi ramify. The spongy layer is finally reached and converted into labyrinths, and here the maternal and fœtal blood meet, separated only by the endothelium of the maternal and fœtal capillaries. Hæmorrhages occur in places. The site of these may be seen in the dog and cat in the region known in the former as the 'green border' and 'green pockets' of the placenta (Marshall). Here the trophoblast finds abundant nourishment to send back to the embryo through the villi in the form of broken-down tissue and cells, which are dealt with by phagocytosis. It will be observed that in the hæmorrhage areas the trophoblast is in direct contact with effused maternal blood. So good is the blood-supply that the glandular secretion from the uterus, so well marked in herbivora, plays a very unimportant part in the nutrition of the embryo of carnivora.

The Yolk Sac or Umbilical Vesicle.—While the vascular connection above described is being effected, the nutrition of the embryo is to an extent looked after by the yolk sac. In birds this contains yolk; in the large majority of mammals it does not, but merely an albuminous fluid which is very soon exhausted. The yolk sac is one of the vestiges of an early ancestor, and is functionally active but for a few days until the circulation with the mother is established. In the sheep, pig, and cow it is of use until the twentieth day of pregnancy; in the mare it persists to about the end of the eighth week. In the dog it is large, and, according to some, persists to birth, though not functional during the whole of the time. Broadly speaking, it functions for about three weeks, but may persist longer, during which time it is unimportant. It is derived from a portion of the ovum which is not set apart for the development of the embryo, and is attached to the latter at the umbilicus through the medium of a stalk which subsequently becomes the umbilical cord; to the mother it is attached by the layer of cells so frequently spoken of as the trophoblast. It contains in its substance some granules; its walls are vascular, and it supplies nourishment to the embryo additional to the material which the trophoblast takes up from the fluid in the uterine cavity, and the material which it extracts from the uterine wall during the formation of the placenta. As the placental circulation becomes more thoroughly established the yolk sac shrinks, and finally forms a part of the umbilical cord. Figures of the yolk sac in the bird and the embryo of the horse at different stages of development are seen in Figs. 260, 261, 264 and 265.

Uterine Milk.—If the placenta be separated from the wall of the uterus, especially in ruminants in the region of the cotyledons, a white or pinkish-white fluid may be expressed, creamlike in consistency, containing protein and fat in considerable quantities, and a small proportion of ash. This is the uterine milk, believed to be peculiar to the ruminant. We have already seen that a fluid secretion from the uterine glands is poured out in greater or less quantities into the uterus of all animals, though it is small in amount in the carnivora; in none does it present the creamy appearance seen in cattle and sheep. It is perhaps permissible to refer to any uterine secretion intended for the nutrition of the embryo as uterine milk, though it is not the same in composition in all species. In that of ruminants rodlike crystals abound which were supposed at one time to be crystals of protein, but the latest view is that they consist of calcium oxalate. In all species of animals the cellular elements of the uterine secretion are abundant, derived from the epithelium of the uterus, its gland ducts, and the extravasation of blood-cells. It is apparent that the composition of uterine milk is perfectly adapted for the phagocytic activities of the trophoblast, and later of the placenta, which transfer the nutritive material to the blood of the embryo. Inasmuch as the cotyledons do not contain glandular tissue, it has been urged that the fluid part of the secretion cannot occur from these projections, but only from the area between the cotyledons. Assheton has shown that in the sheep the glandular secretion diminishes towards the end of pregnancy, in consequence of the destruction of the uterine glands, but that at the upper end of each uterine horn the mucous membrane furnishes an active secretion from its epithelial layer.

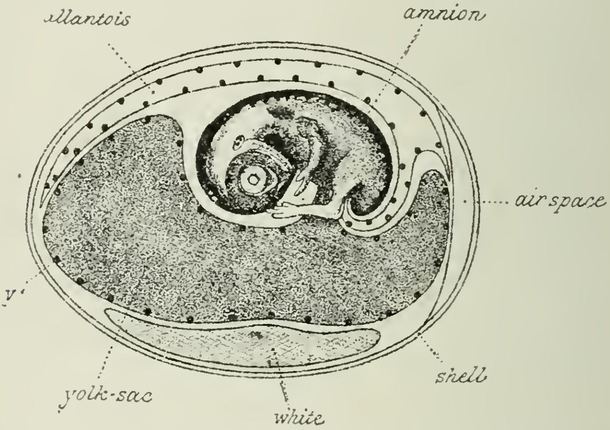

FIG. 261.—HEN'S EGG AT THE NINTH DAY OF INCUBATION (EWART, AFTER MILNES MARSHALL).

Membranes of the Embryo.—We shall first consider the bird, and by so doing prepare the way for a better understanding of the mammal.

If the egg of the hen be examined after incubating nine days, the appearance seen in Fig. 261 presents itself. A chick in an advanced stage of development is bound within a thin tough skin containing fluid; this water-jacket is known as the *amnion*, and its use is to prevent jar when the egg is moved. The supply of food required by the embryo chick during development is contained in the *yolk sac*; to this food-supply the embryo is connected by a stalk through which the nourishment enters its body. The walls of the yolk sac are vascular and connected with the vessels of the embryo. It is through the medium of the vascular wall that the altered yolk is taken up. The chick has another fœtal appendage known as the *allantois ;* it grows out from the body, being connected to the embryo by means of a stalk, and forms a vascular sac through which blood from the chick's body circulates. The allantois in the chick is a breathing organ; the air enters through the pores of the shell, and the blood takes up oxygen from the air surrounding the allantoic sac; an air space also exists at the end of the shell.

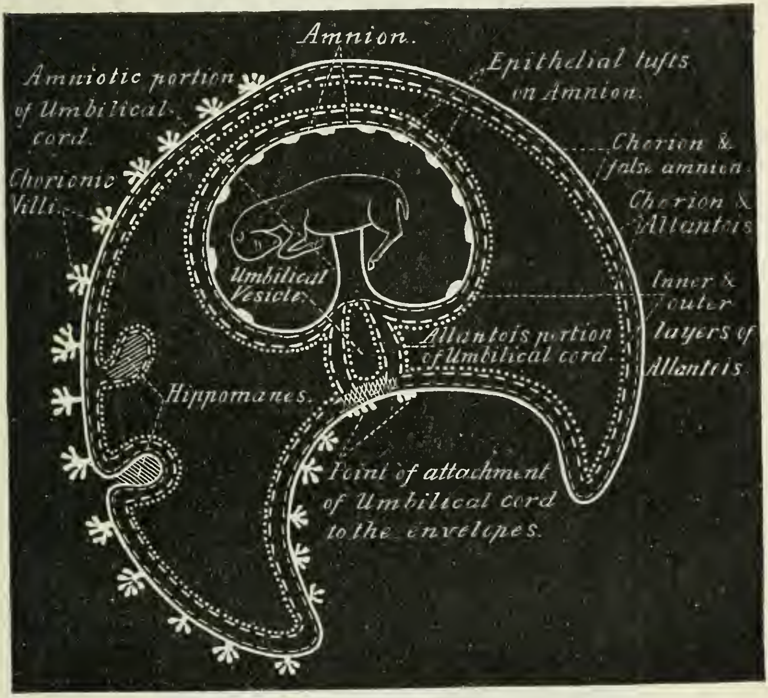
Amnion.
Amniotic portion of Umbilical cord.
Epithelial tufts on Amnion.
Chorion & false amnion.
Chorionic Villi.
Chorion & Allantois
Umbilical Vesicle.
Inner & outer layers of Allantois.
Allantois portion of Umbilical cord.
Hippomanes.
Point of attachment of Umbilical cord to the envelopes.

Fig. 262.—Diagram of the Fœtal Envelopes of a Five Months Horse Embryo (Bonnet).

Amnion.—Precisely as does the chick, the mammal possesses an *Amnion*, derived from a portion of the embryo, which grows completely around its body (Fig. 260), forming a sac containing fluid, the function of which is to act as a water-bed to the fœtus and save concussion. In the horse it is fully formed at the twenty-eighth day. In ruminants the amnion contains a number of white patches, particularly on the cord; these *amniotic plates*

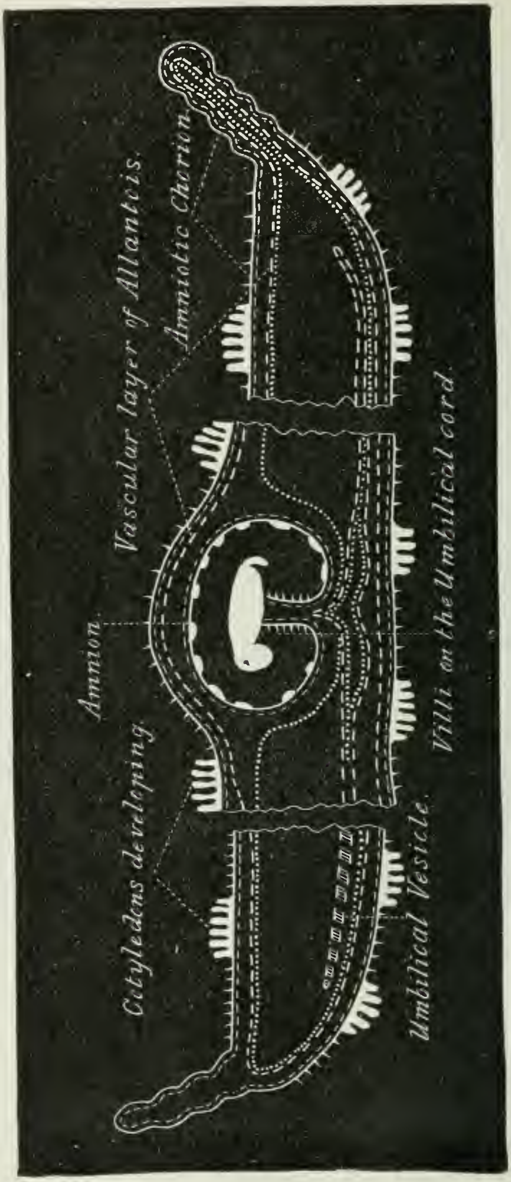
Amniotic Chorion
Vascular layer of Allantois
Amnion
Cotyledons developing
Villi on the Umbilical cord
Umbilical Vesicle

Fig. 263.—Diagram of the Fœtal Envelopes of Ruminants (Bonnet).

Only the central portion and extremities are represented.

are rich in glycogen, so that their function may be connected with the nutrition of the fœtus. Their period of functional activity is probably only temporary, as they undergo atrophy after the sixth month. *Liquor amnii* is an alkaline fluid, yellowish-red during the early days of gestation, but reddish towards the end of it, probably owing to discoloration with fœtal fæces or *meconium.* The fluid contains protein, urea, sugar, lactic acid, keratin, and some salts. Besides these, there are in hoofed animals portions of hoof, and in all animals epithelium and hair derived from the fœtus. The source of the fluid is transudation from both mother and fœtus; indigo blue injected into the veins of the mother stains the amniotic fluid but not the fœtal tissues. During parturition the fluid helps to dilate the os, and lubricates the maternal passage.

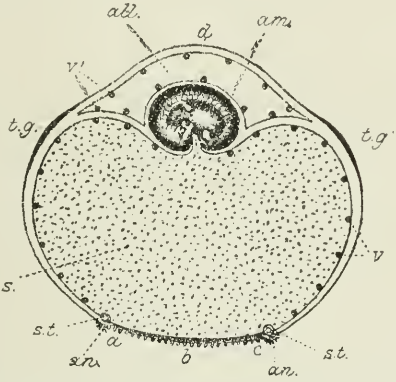

Fig. 264.—Semi-diagrammatic Representation of a Four Weeks Horse Embryo and its Fœtal Appendages, Natural Size (Ewart).

am., The amnion; *y.s.*, the yolk sac, which is vascular (*v*) as far as the circular bloodvessel (*s.t.*), and crowded with granules; *a*, *b*, *c*, the trophoblast; *all.*, the allantois; *d*, sac containing the embryo; *t.g.*, the girdle; *v'*, vessels in wall of allantois. The embryo measures nearly $\frac{3}{8}$ inch in length, and is curved so that the tail lies under the head. The limbs are represented by lobes; the rudiments of the limb skeleton have not yet appeared.

The *Allantois* grows out from the body of the embryo at the future umbilicus (Fig. 260). The part within the body forms the bladder, that outside it forms a sac which in the mare completely envelops the amnion (Fig. 262) on the one surface, and on the other lines the chorion. As it is a complete replica in shape of the chorion, it possesses a body and two horns. In ruminants it is an elongated sac which does not completely line the chorion, though it projects into both horns (Fig. 263). The bladder and the cavity of the allantois are connected by a funnel-shaped canal in the umbilical cord, known as the *urachus.* The remains of this may be seen in the adult as a scar on the fundus of the organ. The fluid found in the allantois is derived from the fœtal urine. In the first instance it is colourless or turbid, later on it becomes brown in tint. This fluid contains urea and a substance known as allantoine; also protein, sugar (levulose), lactic acid, and certain salts. The allantois is the organ of respiration, and to an extent of nutrition. During early fœtal life the vascular wall of the allantois is able to bring the blood of the embryo sufficiently near to that of the uterus to cause an exchange of gases to be effected. Later it furnishes the villi which penetrate into the walls of the uterus, and vascularises the placenta in all domesticated animals. In the mare the function of the allantoic fluid is to provide a second water-jacket for the fœtus. At parturition it acts hydrostatically by dilating the os uteri and vaginal passage.

In the allantoic fluid of the mare, or attached to the wall of the sac, are certain peculiar masses termed *hippomanes ;* these are doughy, oval masses contained in a capsule, yellowish-brown in colour, and about 2 or 3 inches in length. Their origin and use are quite unknown. It is commonly believed that these bodies are found in the foal's mouth at birth, but this is a fallacy, for they belong to the allantoic sac, whereas the fœtus lives in the amnion.* Hippomanes have also been observed in the cow.†

The *Chorion*, or outer covering of the fœtus envelops the two sacs previously mentioned. In shape it is an exact replica of the uterus, and consists of a body and two horns. In the equine it is closely adherent to the uterine wall through the medium of the minute villi which stud its outer surface; its inner surface is lined by the allantois. In ruminants also it consists of a body and two horns, but otherwise differs greatly in appearance from that of the horse, as it is vascular only in the region of the cotyledons. In the pig and dog the chorion is an elongated sac without body or horns. Through the umbilical cord it forms the vascular connection between the fœtus and the mother, while the villi on its surface, furnished by the allantois growing through (Fig. 265), project themselves into the mucous membrane of the uterus, and are thus brought close to the maternal vessels. The chorion is the vascular covering through which the blood from the fœtus is conveyed to the mother for the purpose of getting rid of its carbon dioxide, and receiving in its place oxygen and nutriment. The villi in the horse are not more than one-eighth of an inch in length (Ewart), and consequently the chorion is readily detachable from the interior of the uterus at birth. The villi of the cotyledons in ruminants are also not difficult to separate.

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* Mr. F. T. Harvey informs me he has frequently felt in the mouth of the foal before delivery and has never found hippomanes within it.

† It is a curious fact that even at the present day, in some country districts, hippomanes are sought for in virtue of the properties they have been supposed to possess from time immemorial—viz., for use as love philtres.

Death of the Embryo.—An impregnated ovum which has become linked up with the mother in the manner described in the previous pages does not always necessarily live through the whole process of development. It may die from failure of nutrition, the causes of which are various and some not clearly understood. In the pig, for example, living and atrophied fœtuses may be found side by side in the uterus (Hammond).* In the mare death of the embryo is more serious, especially in the case of thoroughbred stock, whose fertility is extremely low, and where the date of foaling is all-important. 'Breaking service,' as it is known in the language of the stud, or detachment of the embryo, is common from the sixth to the ninth week, and has formed the subject of special inquiry by Ewart.† He has shown that the embryo at *four weeks old* is held in position on the uterine wall by the layer of trophoblast cells (Fig. 264, *a*, *b*, *c*) strengthened by a ring of tissue (*an.*) which crops up around them. The ovum is suspended in the uterine horn upside down by the stalk of the yolk sac to which the trophoblast cells are attached. This position, which is also the normal one in man, would appear to invite detachment. By the *fifth week* a girdle (Fig. 264, *t.g.*), peculiar to the horse only, has appeared around the equator of the ovum, and is adherent to the uterine wall. It is an additional means of security, and is now most useful, for the trophoblast area is suffering a reduction in the size of its attachment. At the *sixth week* the weight of the embryo is twice that at the fifth week; the trophoblast adhesion (Fig. 265, *a*-*c*) continues to get smaller, and the girdle (*t.g.*) has moved from the equator to the pole—*i.e.*, nearer to the trophoblast. In other words, the attachment is less secure; nutrition also is failing, as shown by the reduction in the size of surface which unites the yolk sac to the uterus, and the chances of the ovum being cast off should the mare be 'upset' from any cause (such as recurrence of œstrus), are considerable. Ewart regards the end of the sixth week as the period at which the primitive ancestors of the horse were born. During the *seventh week* the function of the yolk sac is almost exhausted, and the allantois is not yet fully developed, though three times larger than it was during the preceding week. The girdle, however, is stronger. By the middle of the *eighth week* the allantois has put forth the villi which eventually form the chorion, and these are lodged in pits in the uterine mucous membrane; if the development of these fail from any cause, the embryo is doomed. When the embryo has reached the *ninth week* the placental circulation is established and it is now safe.

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* *Journal of Agricultural Science*, vol. vi., part iii., 1914.

† 'A Critical Period in the Development of the Horse,' by Professor Cossar Ewart, M.D., F.R.S., 1897. This paper should be read by all interested in breeding, and especially by the veterinary profession. It is through this communication that our knowledge of the horse embryo from the fourth to the ninth week of development is so complete.

The Umbilical Cord.—This is the channel by which the blood is passed from fœtus to mother and from mother to fœtus. It contains two arteries and a vein; in ruminants two veins. In its substance is enclosed the now unnecessary yolk sac; the cord also contains the urachus, the tube leading from the fœtal bladder to the allantois. On reference to Fig. 262 it will be seen that in the horse there is an amniotic and allantoic portion of the cord. The amniotic portion is by far the longest; it lies slack in the amniotic cavity, and presents the appearance of a twisted rope. The cause of the twisting is unknown. The allantoic portion is shorter, less twisted, and terminates in the chorion in the upper part of the wall of the uterus between the two horns. The entire cord is covered by a layer of connective tissue known as Wharton's jelly.

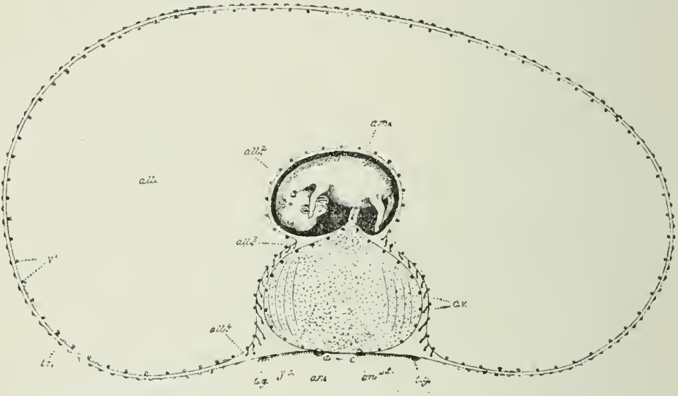

FIG. 265.—A SEVEN WEEKS HORSE EMBRYO, HALF NATURAL SIZE (EWART).

all., Allantois, which has greatly increased in size; *am.*, amnion; *c.v.*, non-vascular villi (cœlomic) lying between the allantois and the yolk sac, not hitherto found in any mammal, and function unknown; *y.s.*, yolk sac; *a-c*, the trophoblast; *v'*, villi of allantois preparatory to growing through the wall and forming *t.t.*, the chorion; *t.g.*, the girdle now moved to the pole; *s.t.*, circular bloodvessel; *all.*², allantois in connection with amnion; *all.*³, *all.*⁴, part of allantois in connection with the yolk sac.

In ruminants, owing to the elongated character of the allantois, the umbilical cord passes to the chorion direct after traversing the amnion, so that there is only an amniotic portion (Fig. 263).

Fœtal Circulation.—With the formation of the fœtal circulation the blood follows a course altogether different to that in the vascular area of early embryonic life. Impure blood that has circulated through the tissues of the developing young is brought to the placenta by the umbilical arteries, these acting to the fœtus as the pulmonary arteries to the adult. After an interchange of gases and a renewal of food supply, the blood is carried back to the fœtus by means of the umbilical vein, or veins, found in the cord. The vein enters the body at the navel or umbilicus, passes forward along the floor of the abdomen, reaches the falciform ligament of the liver, travels along the free edge of that structure, and empties itself into the portal vein. After birth the remains of the umbilical vein are found as a thickening at the free edge of the falciform ligament, and form the round ligament of the liver. In ruminants the umbilical veins are two in number, but they unite to form a single vessel on entering the body. The vessel thus formed passes along the abdominal floor towards the falciform ligament to occupy the same position as in other animals, but before reaching it, it detaches a large branch—the *ductus venosus* (Fig. 266, *d.v.*)—which passes forwards to join the posterior vena cava. After the blood has circulated in the liver it leaves by the hepatic trunks, and is poured into the posterior vena cava, where it meets with the blood in that vessel, and is thus conducted to the heart. Thus in the horse the whole of the fœtal blood passes through the liver before reaching the heart by the posterior vena cava. In ruminants and the dog, part of the blood passes through the liver, subsequently gaining the posterior vena cava, and part goes direct to the posterior vena cava through the ductus venosus.

In the fœtal heart the cavities of the right and left auricles are in communication by means of a foramen, the *foramen ovale*. This opening in many animals is provided with a valve—the Eustachian—that stretches from the mouth of the posterior vena cava to the annulus or thickened border of the foramen ovale; the valve is absent from the hearts of the fœtal horse and pig. The function of this valve is to direct the blood-stream into the left auricle; from there it passes into the left ventricle, and thence into the aorta. The greater portion is driven into the vessels that supply the head, neck, and fore-limbs (anterior aorta and branches), and is conveyed to the head and anterior portion of the body; the remainder passes backwards in the

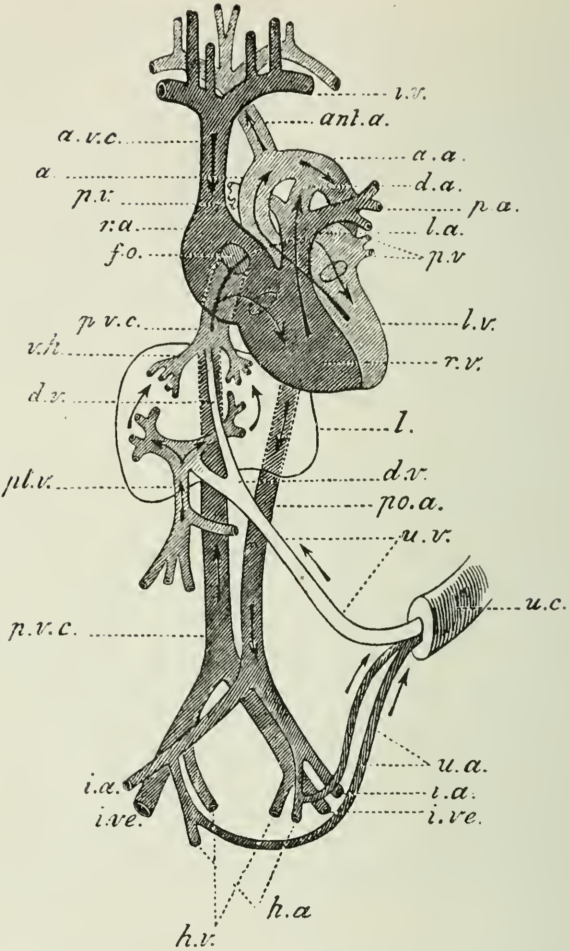

FIG. 266.—DIAGRAM OF THE FŒTAL CIRCULATION (ELLENBERGER).

u.v., Umbilical vein; *d.v.*, ductus venosus; *pt.v.*, portal vein; *l.*, liver, shown in outline; *v.h.*, hepatic veins; *p.v.c.*, posterior vena cava; *r.a.*, right auricle; *f.o.*, foramen ovale; *r.v.*, right ventricle; *p.a.*, pulmonary artery; *p.v.*, pulmonary veins; *d.a.*, ductus arteriosus; *l.a.*, left auricle; *l.v.*, left ventricle; *a.*, the aorta; *a.a.*, arch of aorta; *ant.a.*, anterior aorta; *i.v.*, innominate veins; *a.v.c.*, anterior vena cava; *po.a.*, posterior aorta; *i.a.*, iliac artery; *h.a.*, hypogastric artery; *u.a.*, umbilical arteries; *i.ve.*, iliac veins; *h.v.*, hypogastric veins; *u.c.*, umbilical cord.

The diagram actually represents the fœtal circulation in ruminants; to make it applicable to the horse the ductus arteriosus (*d.v.*) must be supposed to be removed; the whole of the blood then traverses the liver by the union of the umbilical vein (*u.v.*) with the portal vein (*pt.v.*). The arrows indicate the course taken by the blood. Observe that the stream entering the right auricle divides, part passing into the right ventricle, and part into the left auricle through the foramen ovale (*f.o.*).

posterior aorta. The head, it will be noticed, receives almost pure blood. After the fluid has circulated in this part of the body, it is returned to the right auricle of the heart by the anterior vena cava. From the right auricle it passes to the right ventricle, and from this cavity it is pumped into the pulmonary artery. The lungs, however, are not functional, and are more or less solid organs; consequently, they are not yet prepared to receive the blood. This must therefore take another course than through the lungs. The course is provided by the *ductus arteriosus* (Fig. 266, *d.a.*), a short vessel uniting the pulmonary artery to the aorta, and thus bringing their lumina into communication. By this conduit the blood enters the posterior aorta. and is conveyed to the hinder parts of the body and to the placenta.

The allantoic or umbilical arteries (Fig. 266, *u.a.*) convey the blood from the fœtus to the placenta. These arteries are branches of the internal pudics, or of the parent vessels, the internal iliacs, and during intra-uterine life they are larger than the parent vessels. Soon after birth, however, their walls become thickened, their lumina are lost, and they become impervious to the passage of blood. In the adult they are recognised as the thickened cords found in the lateral ligaments of the bladder. The ductus arteriosus just prior to birth has a lumen easily receiving an ordinary cedar pencil but it steadily diminishes until, at about a month after birth it is no greater than the diameter of a knitting-needle. It is probable that little blood passes this way after birth, but the exact period of total occlusion is unknown. Similarly, the foramen ovale is blocked up by the development of a membrane, which may be pulled out with the forceps shortly after birth, and then resembles in shape an old-fashioned lace nightcap or cowl. When undisturbed, it lies in a heap, filling up the foramen.

The short cuts in the fœtal circulation—viz., the *ductus venosus, ductus arteriosus,* and *foramen ovale*—exist mainly with the object of insuring that the purest blood reaches those organs which require it most. The heart, head, and fore-limbs receive blood which is much purer than the blood circulating through the hind-limbs and abdominal viscera, for the brain must be well fed.

Fœtal and Maternal Nutrition.—This subject is very imperfectly understood; we do not know with anything like precision what the mother loses during pregnancy, nor the form in which it is lost. This is due to the great difficulties connected with such an inquiry, and probably to the fact that the nutrition of the fœtus is not the same in all animals. The mother's blood does not circulate through the fœtus, yet the mother supplies, by the methods outlined in the previous pages, all that is required for the process of development, growth, and the purification of the blood. But the fœtus is not without its share in the matter. It is furnished with its protein, fat, carbohydrate, and salts, but the conversion of these into body tissue is the work of the fœtus. The nutriment may be received in a ready-made form, but there is a good deal of evidence to show that the fœtus is not always provided with the fully formed material, but has to elaborate it in its own tissues. Nutrition in the early stages, before the final circulation is in working order, is carried out in the trophoblast and by absorption through the outer layer of the embryo. The materials available through the trophoblast are the cellular elements of the mother's blood, masses of protoplasm, and in some animals (carnivora) actual tissue from the walls of the uterus. The nutriment absorbed by the outer covering of the embryo is derived from the uterine secretions of the uterine glands, especially in herbivora, and from the blood extravasations into the mucous membrane.

When the placental connection is established, the work of taking up protein is easier; in fact, in the sheep nucleo-protein is formed in the cotyledons; the placenta also furnishes glycogen in the case of the carnivora, but not in ruminants; it also furnishes fat, the placenta of the herbivora being especially rich in this substance, while an abundance is obtained through the uterine milk.

The fœtal tissues contain glycogen. The carbohydrate metabolism is very active in view of the fact that the energy it yields is utilised in the building up of the embryo. The mucin-holding tissues, so evident in the fœtus, contain a carbohydrate group which may be derived from glycogen. It is not clear in what way glucose is transferred from the mother to the fœtus; it is supposed to pass by diffusion, but this is probably not correct, as the allantoic fluid of the ruminant and the blood-serum of the fœtus contain lævulose. The glycogenic functions of the liver are probably established very early in fœtal life. The secretion of bile begins early, and is discharged into the intestines as *meconium*. The liver, indeed, in the fœtus is an extremely active organ, as may be judged from its size, and it is accordingly abundantly supplied with blood.

The supply of salts is obscure; the whole question requires working out, but the drain on the mother is no doubt considerable. Iron obtained from broken-down hæmoglobin is stored in the liver of the fœtus for the synthesis of hæmoglobin, and, according to Bunge, in extra-uterine life to supply the deficiency of iron in the mother's milk.

The placenta is an efficient filter for many pathological substances, though not for all. The tubercular mother does not convey tuberculosis to the fœtus, though the syphilitic mother can infect her infant. Colouring matter may not be arrested by the placenta. The bones of the fœtus are stained if madder be administered to the mother.

The metabolism of the fully developed fœtus may be low, the oxygen content of its arterial blood being below that of the mother's; this is true for the sheep, and probably all herbivora, though not so for all animals. In the sheep the umbilical vein of the fœtus may contain 6·3 per cent. oxygen, while the arterial blood of the mother contains 20 per cent.

There is one feature in the matter of intra-uterine nutrition which is unquestionable. It is beyond doubt, both from direct experiment on animals and the practical results obtained in breeding, that if the mother during pregnancy is insufficiently nourished, the offspring is stunted in its growth. The question of growth has been touched on elsewhere (p. 376). The main feature of intra-uterine growth is its enormous energy during the early stages of gestation, and its sudden fall when all the tissues and membranes are laid down and the final system of blood-supply fixed. It is said that in the rabbit between the ninth and fifteenth day 704 per cent. is added to the weight daily, and for the fifteenth to the twentieth day only 212 per cent. Ewart tells us also that the eight weeks' embryo of the horse is twice the length and four times the weight of the seven weeks' embryo. It is evident that if this rate of growth were maintained throughout the whole of intra-uterine life, the fœtus would exceed the size and weight of its dam.

All animals within the uterus are carnivorous.

Causation of Sex.—There are many theories accounting for the determination of sex, some of which have been handed down from antiquity, such, for instance, as the right and left ovary or the right and left testicle furnishing sex of a definite type. The theory of the mean vigour of the male and female cells at the time of conception has found a good deal of support, a low mean vigour, it is said, leading to male and a high vigour to female progeny. Quite recently it has been stated that in his day's work a vigorous stallion produces male progeny at the beginning of the day and female progeny as his ardour becomes exhausted. No attention need be paid to this statement; it is refuted by the practical results of breeding.

In all animals an examination of the birth-rate shows that the two sexes are produced in approximately equal proportions.

It was Heape who first authoritatively stated that there was no such thing as a purely male or purely female animal, but that each sex contained a dominant and recessive character, excepting *hermaphrodites*, in which both sexes were equally represented. As evidence of this, he drew attention to the assumption of male characteristics in old females and of female characteristics in old males of the human species—facts apparent to all. The same may be observed in the lower animals; attention has been drawn at p. 746 to the effects of castration in young cats of both sexes in the production of a skull of male type in the female, and of female type in the male; to the effect of caponing in the production of female plumage, and in the absence of crowing; capons have even incubated eggs and reared the resulting progeny. Interference with the ovaries in birds has led to the production of male characteristics, and there is much evidence of a similar kind in all animals. In all such cases it is evident that the recessive sex asserts itself when the dominant sex becomes weakened. Every animal, therefore, contains in its cells the factors for its own sex and also those for the opposite sex.

Everything points to ova and spermatozoa being sexual; that is to say, there are male and female ova, male and female spermatozoa. Microscopic differences in the number of chromosomes in spermatozoa give additional support to this, for it is known that there are spermatozoa containing the full number for the species and others from the same animal containing one extra, or *accessory*, as it is termed. This has been shown to be true for the horse and other animals by Wodsedalek (see p. 753). Spermatozoa containing the 'accessory' chromosome are, according to this authority, female-producing; he further states that the spermatic secretion contains male and female producing spermatozoa in equal numbers. It would therefore appear evident that the sex of the offspring is fixed at the time of fertilisation, and no subsequent influence can alter it; the ovum in which one sex is dominant must be fertilised by a spermatozoon in which the opposite sex is dominant; whether the sex be determined by the ovum or the spermatozoon depends upon which is the more powerful of the two.

Heape has shown in his study of the ovary of the rabbit* that ova may degenerate, and that one of the chief causes of degeneration is imperfect nutrition (see pp. 745 and 775); in this way, it is thought, a selective action effects a variation in the proportion of the sexes of the ova produced. Where no such selective action occurs in the ovary the proportion of the sexes in ovarian ova produced is governed by the laws of heredity.

That one parent may be prepotent† over the other in the production of sex is a matter of everyday observation, and this prepotency may be shown in the female even when the sires are different. It is well known, for instance, that a cow may produce offspring always of one sex, in spite of the fact that each year she may be mated with a different sire.

Twin and Multiple Births.—We have already seen at p. 756 the number of ova shed at an œstrus period. Multiple births are the rule in the pig, dog, and cat. Twin births are frequent in sheep, but the normal number of progeny produced by the mare and cow is one. Twin births in the mare are about eight per thousand in thoroughbred stock. In cattle (especially Shorthorns) they are more frequent. Human twins may be formed from a single egg (true or identical twins), or from two eggs. If from a single egg, the amnion is common to the two; there is a single chorion, but two umbilical cords. If from two eggs the membranes are not only distinct, but the placenta is double. In man, twins formed from a single egg are invariably of the same sex; if resulting from the impregnation of two eggs they may be of the same or of opposite sexes. The monstrosities met with in obstetrical practice are commonly found in identical twins. There is a form of twin birth in cattle which is of exceptional interest: the sexes of the twins are opposite; the male is potent, the female generally sterile. The sterility is due to an undeveloped condition of the internal generative organs, the external organs appearing normal. Such a heifer-calf is known as a **free-martin.** The problem of the development of this imperfect animal has occupied the attention of morphologists for over one hundred and fifty years, and the question is not yet settled.

Berry Hart concluded that the two embryos arose from a single egg, and that in consequence the genital cells of a single ovum were insufficient to furnish each animal with a complete generative apparatus. As a consequence, one of the twins (the male) is perfectly developed, the other imperfectly. Hart pointed out that the imperfectly developed animal, though apparently a female, was in reality an imperfectly developed *male*. It is not an **hermaphrodite**; such a creature must be in possession of both male and female sexual organs, and produce both ova and spermatozoa.*

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* 'Ovulation and Degeneration of Ova in the Rabbit,' *Proceedings of the Royal Society*, B vol. lxxvi., 1905.

† In Mendelian phraseology the expression 'dominant' is employed.

The question has been examined recently by F. Lillie and Catherine Chapin,† and the conclusions arrived at were that the twins arose from *different* eggs, one from each ovary, and that the sex of the free-martin is *female*, and not male. It is pointed out that cattle twins have a common chorion and complete vascular anastomosis between the pair, with the result that intermixture of the blood of the two fœtuses results. Owing to this vascular connection the sex hormones of the male embryo enter the circulation of the female twin and inhibit the development of the female organs. In those rare cases where the female is found fertile, the two chorions are unfused and the twin circulations are distinct.

Superfecundation and Superfœtation.—Superfecundation is a term applied to indicate that two eggs have been impregnated at different periods at *a short interval*—for example, the classical case of the mare which produced twins, a horse and a mule foal, as the result of coitus with first a stallion and then a donkey. This case is not unique.‡ Superfœtation is the impregnation of a second egg at a *period remote* from the first act of fertilisation. This is not unknown in the cat, but does not appear to have been met with in the larger domesticated animals. It has recently been urged by Sumner,§ as the result of observations on mice, that spermatozoa may retain their fertilising power for days or weeks after reception into the uterus or Fallopian tubes, and that a later copulation with a different partner may coincide with a conception in which the earlier insemination is really the effective one. Sumner suggests that some alleged instances of telegony may thus be explained.

The **Duration of Pregnancy** appears to be based on no fixed law. Judging from the length of time the elephant is in gestation, it might appear that body size had an influence, but against this is the fact that the ass carries her young longer than the horse, while, whether it be a toy terrier or a Newfoundland, a dog goes from sixty to sixty-six days. It certainly does appear that among animals of the same species breed has an influence in the matter; different herds of cows vary from 277 to 288 days, Merino sheep average 150 days, Southdowns 144 days. It is not clear why, of two rodents, the guinea-pig should require a period of gestation twice as long as the rabbit.

The only point which appears fixed is that animals born in a stage of development when they can immediately follow their mothers (herbivora) have a longer period of gestation than those born helpless, as in the case of the carnivora.

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* Hermaphroditism may be produced experimentally in rats by implanting ovary into testis, and by transplanting ovary and testis into young castrated animals (see also p. 747).

† *Journal of Experimental Zoology*, vol. xxiii., 1917.

‡ See Fleming, *Textbook of Veterinary Obstetrics*.

§ *Biological Bulletin*, vol. xxx., 1916.

The following are average periods of gestation:

Elephant	20 months.
Mare*	11 months, and liable to vary within relatively wide limits.
Ass†	358 to 385 days.
Zebra	358 to 385 days (Ewart).
Cow‡	40 weeks.
Sheep	21 weeks (average).
Camel	45 weeks.
Pig	16 weeks.
Dog	60 to 66 days.
Cat	63 days.
Rabbit	32 days.
Guinea-pig	63 days.

Parturition.—The cause of parturition is unknown. The fœtus having reached its full stage of development, changes of an obscure nature take place which lead to its expulsion. During uterine life the equine fœtus is lying on its back on the floor of the mother's abdomen, with its chin on its chest, the fore-legs bent at the knee, and the hind-legs in the right horn (Fig. 267). Preparatory to birth the fœtus changes position and turns on its side, so as to assume, first a lateral position (Fig. 268), and lastly an upright one (Fig. 269), by which the fœtal and maternal spines are brought nearer together. To assume this position the fœtus has had to make a complete revolution; it is now brought with the muzzle and fore-legs in the direction of the pelvis (Fig. 269), and dilatation of the passage follows. In the cow the fœtus lies on its back on the floor of the abdomen as in the mare, but somewhat crooked—viz., the head inclining towards one side, and the hind extremities towards the other; in all other respects its position resembles that of the fœtus of the mare. The alteration in the position of the fœtus does not occur through its own movements, but by the contraction of the uterus; on the other hand, the stretching of the limbs is the result of fœtal movement.* There can be little doubt that the revolution of the fœtus prior to birth is the explanation of the complete torsion of the neck of the uterus and vagina which is sometimes found in both the cow and mare.

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* Tessier, in a memoir on the period of gestation presented in 1825 to the Royal Academy of Science in Paris, stated that in 582 mares, after one sexual congress, the shortest period of gestation was 287 days, the longest 419 days, a difference of 132 days. In 312 mares which visited the horse several times, the shortest period of gestation, calculated from the last cover, was 290 days, the longest 377 days, a difference of 87 days.

L. Dupas, *The Revue Vétérinaire Militaire*, June, 1913, records the gestation period of the mares in a breeding depot. He places it at from eleven to eleven and a half months, the total number of observations being 415.

20·96 per cent. of the total births occurred between the 331st and 340th day.
33·01 ,, ,, ,, ,, ,, 341st ,, 350th ,,
23·37 ,, ,, ,, ,, ,, 351st ,, 360th ,,
9·63 ,, ,, ,, ,, ,, 361st ,, 370th ,,

But for these precise figures, we should have thought it unlikely that over 9 per cent. of the births occurred as late as a year after conception.

† Tessier gives the period of two asses, one being 12 months 20 days, the other 13 months 1 day; and these agree very closely with Sutherland's observations (*Veterinary Record*, October 13, 1894), quoted in the text above.

‡ Of 1,131 cows, the average period observed by Tessier was 240 days; the longest was 231 days (*Veterinarian*, vol. i., 1828).

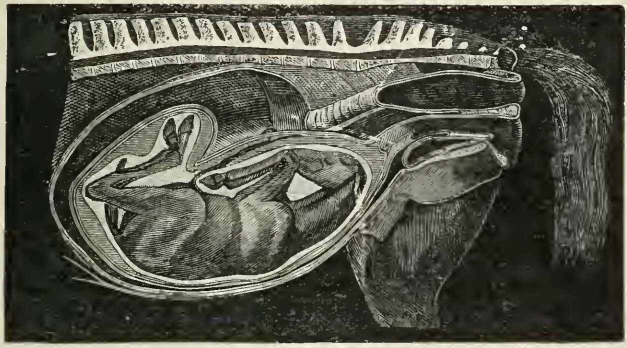

FIG. 267.—THE POSITION OCCUPIED BY THE EQUINE FŒTUS DURING INTRA-UTERINE LIFE (FRANCK).

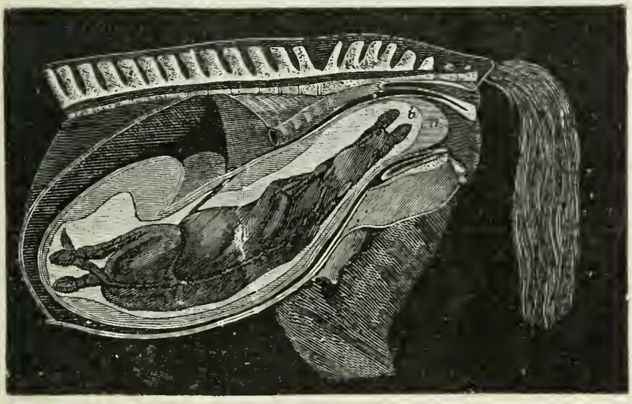

FIG. 268.—THE FIRST STAGE IN THE REVOLUTION OF THE FŒTUS: LATERAL POSITION. THE OS IS DILATED BY THE MEMBRANES WHICH HAVE NOT YET RUPTURED (FRANCK).

a, The allantois; *b*, the amnion.

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* This description of the change in the position of the fœtus preparatory to birth is taken from Ellenberger's ' Physiologie ' (after Franck).

The dilatation of the os is assisted by the amniotic and allantoic fluids. Each contraction of the uterus is accompanied by a pain; the pains last from fifteen to ninety seconds, and the interval between them is from two to four minutes. The contractions of the uterus, from horns to fundus and thence to the os, occur under the influence of a centre in the lumbar portion of the cord; they are not under the control of the will, and occur even though the animal be unconscious, or the spinal cord divided in the lower cervical region (dog). In multiple births the passage of one fœtus is greatly assisted by the pressure of the one immediately behind.

The mare is remarkable for the rapidity with which delivery is effected; ruminants, on the other hand, are often very slow and in labour for hours. Parturition in the mare is accompanied by a complete separation of the chorion from the uterine wall; this is the explanation of why any difficulty in delivery invariably sacrifices the life of the foal. In ruminants, on the contrary, the circulation between the mother and fœtus is to the last kept up by the gradual separation of the cotyledons, so that, though the process may be delayed several hours, the animal is generally born alive. The cause of the first respiration of the fœtus is dealt with at p. 142.

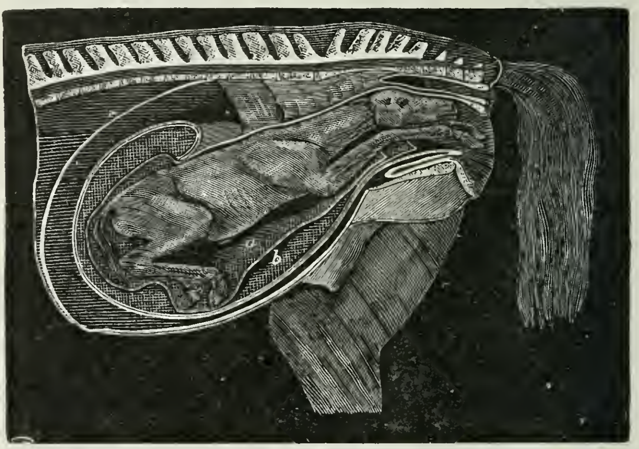


Fig. 269.—The Revolution completed, Membranes ruptured, and Foal in the Normal Position for Delivery (Franck).

a, The amnion; *b*, the allantois.

Separation of the Membranes.—After the birth of the animal the fœtal membranes have to be cast off. In the mare this occurs very early, owing to the shortness of the villi; in cattle, delay is common. Retention of the membranes leads to their decomposition *in utero*, resulting in septic poisoning. The membranes are expelled by a contraction of the walls of the uterus, which, while driving out what is now a foreign body, also closes the vessels and controls hæmorrhage. The membranes are subsequently eaten by the mother in all animals excepting the horse (see p. 796).

Involution of the Uterus.—The most remarkable change occurs in the uterus in regaining its normal or almost normal size. The shrinking of this large sac, which reaches as far forward as the diaphragm, rapidly occurs. The immensely thickened walls are daily reduced; in the case of the mare, if the uterus be examined a few days after parturition it is difficult to believe that it ever contained a foal and at the ninth day the animal experiences œstrus. It is obvious from what has been said at p. 765 that the nature of the connection between fœtus and mother must influence the length of time involved in involution; for example the destruction of the mucous membrane of the human womb renders its interior a veritable wound. It has been supposed that involution is carried out under the influence of a hormone secreted by the corpus luteum. Contraction of the walls of the organ is assisted by suckling.

Section 2.

The Secretion of Milk.

Mammary Glands.—In all animals the mammary glands have a common structural arrangement; there is the pinkish-grey gland substance separated by septa of fibro-elastic tissue derived from the capsule of the gland itself, and linking up the gland tissue into lobes, and these last into lobules. The lobules are built up of secreting alveoli, each alveolus possessing a tubule; these by uniting furnish a duct for each of the numerous lobes, the ducts opening into a sinus. From the sinus, or *milk cistern*, one or more tubes, according to the species of animal, penetrate the teat. There are as many glands as teats. The skin of the gland is firm, thin, and hairless, and between the right and left glands is a septum of fascia, which not only divides the glands, but supports them in their inverted position.

In the *mare* the skin of the mammary gland has a greasy feel owing to the number of sebaceous glands in that structure; the milk cistern is small, the teats are short, and each is penetrated by two or three lactiferous ducts. The mammary glands, even in a state of activity, are small, and this insures that locomotion is not interfered with.

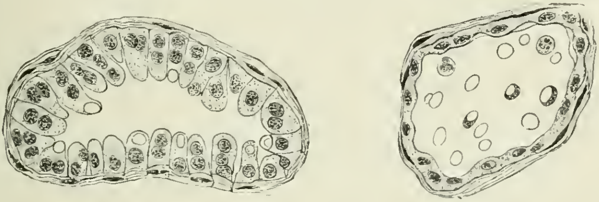
In the *cow* there are four glands arranged as pairs on the right and left; these four glands are usually described as quarters. The pair of glands on the right are divided from those on the left by a suspensory septum. There is no communication between the right and left glands, but the two quarters on the same side of the body are described as communicating. though Sisson states that the injection of coloured fluids into the teats demonstrates that the cavities drained by them do not communicate. The milk cistern in the cow is large and capable of holding from a half to one pint of fluid; where it communicates with the teat it possesses a sphincter muscle over which a little control can be exercised. The teat is penetrated by a single canal which possesses a sphincter at the outlet; the sphincter of the teat is not under voluntary control. The teats are about 3 inches in length.

The milk ducts which drain the lobes and open into the cistern are each provided with a sphincter which is under voluntary control, so that a cow may withhold her milk at pleasure; if her calf has been brought up with her she may refuse to yield any milk in its absence (see in this connection p. 610). No animal, however, has the power to discharge the milk from the gland, and when, owing to accumulation, the tension becomes extreme, pain is produced. The glands in the cow are of variable size; in deep milkers they are enormous. The total volume of the four glands in the cow is said to be about 6,700 c.c., of which 3,000 represent spaces capable of holding milk. In the goat the udder is relatively larger than in the cow.

In the *sheep* there are a pair of glands; in the *pig* ten or twelve arranged in two rows, each teat having two ducts; in the *dog* the glands are ten in number, the teats being penetrated by several openings.

It has been supposed that teats additional to the number normal to each animal indicate fertility.

The Secretion of Milk.—The real work of the mammary gland takes place in the cells found in the follicles of the lobules, but it is not yet settled in what way these cells contribute to the secretion. It has been suggested that they are broken down in the alveolus and their contents elaborated into milk. The resemblance of the mammary to sebaceous glands affords this view some support. A second view is that the cells are not destroyed, but excrete their contents; and the third and most likely theory is that there is a combination of the two processes. In Fig. 270 are seen the loaded and discharged glands of the dog. In the active condition the cells are large and columnar, with one or more nuclei; fat cells are apparent at the free borders of the cell. In the discharged gland the lumen is large, the cells flattened, each containing a single nucleus, while in the lumen of the glands are corpuscular elements. It would appear that the cells do undergo partial disintegration followed by rapid reconstruction, that the fat is extruded as globules, and that the detached portion of the cell furnishes the protein, sugar, and salts. The cellular elements of the lobule elaborate all the constituents of milk from the circulating blood and lymph. This appears to be quite clear, for neither casein nor milk sugar occur in any other tissue of the body, and the ash of milk differs from the ash composition of the blood-lymph, so that the salts are not merely filtered off.



Loaded. Discharged.

FIG. 270.—MAMMARY GLAND OF DOG DURING LACTATION, AFTER HEIDENHAIN (WALLER).

The development of the mammary glands at puberty is brought about by a hormone secreted by the ovary; if these be removed in a non-pregnant animal the glands fail to develop. The enlargement of the glands as the period of parturition approaches is a different question. The experiments of Lane-Claypon and Starling have shown that this development is effected by a hormone contained in the body of the fœtus, which, after absorption by the maternal blood, stimulates the growth of the mammary gland. This substance does not produce a secretion of milk; on the other hand, it inhibits it; it is not until the womb is empty that, in consequence of no further fœtal hormones being produced, the secretion of milk begins. The experimental evidence is sufficiently positive, but there are yet to be explained certain phenomena connected with the production of milk, in which the fœtal hormone can play no part in organising the mammary gland for secretion. For example, it is beyond all doubt that a mule may yield milk and rear a foal. Obviously the foal is a stranger. By what process was the mammary gland of the mule rendered fit for lactation? Milk may occasionally be expressed from the breasts of children and of fillies shortly after birth; this is less difficult of explanation, for the hormone which has been preparing the glands of the mother has originated in the fœtus. Mr. H. Gray informs the writer that he has frequently observed a bitch may come into milk about nine weeks after œstrus, not only though non-pregnant, but without coitus having occurred. She may prepare her bed and even suckle the puppies of another should she get the opportunity. The same observer has seen ewe lambs in the autumn come into milk when fed on young clover. Marshall* states he knew a mare which had never had a foal which could be made to yield milk at any time for years. Heape, in consequence of this class of case, holds the view that the source of the stimulus which excites the activity of the mammary glands must be looked for in the ovary. The rudimentary teats of the goat and sheep, and even of a bull, have been known to produce milk.† A dog (with retention of the testicles in the inguinal canal) has been known to secrete milk, and to be followed about as if in œstrus (Gray). Some evidence has been brought forward to show that mammary growth and milk secretion are under the control of the nervous system, but the severance of all nervous connection prevents neither the development of the gland nor the subsequent secretion of milk. The gland has been transplanted in the guinea-pig to the neighbourhood of the ear, and functioned at the next parturition. Nevertheless, in the absence of a nervous connection it is difficult to explain the uterine contractions which occur in a recently emptied uterus during suckling.

The stimulus to milk secretion is suckling; no artificial method can completely take its place. While sucking is occurring milk is being secreted under its stimulus (see also p. 796).

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* 'Physiology of Reproduction.'

† 'The Breeding of Animals,' F. B. Mumford; also Marshall, *loc. cit.*

Composition of Milk.—The milk of the herbivora has an alkaline reaction, that of carnivora is acid. Fresh cow's milk may be *amphoteric*—that is to say, give both an acid and an alkaline reaction to test paper, owing to the presence of acid and alkaline salts. In the cow the specific gravity varies from 1·028 to 1·034; in the mare, 1·029 to 1·039. It is increased by caseinogen and dissolved substances, and decreased by the presence of fat. A high percentage of fat (cream) in milk accordingly lowers the specific gravity of the fluid. The yellowish-white colour of milk is due to carotin and xanthophyl obtained from green food. The fat in milk is in the form of an emulsion; an emulsion being a subdivision of oil in a hydrated colloid. The proteins are in colloidal solution, the sugar and salts in true solution.[*]

The following table given by Heineman is compiled from various sources:

	Water.	Casein.	Albumin	Total Protein.	Fat.	Sugar.	Ash.	Total Solids.
Man - -	87·58	0·80	1·21	2·01	3·74	6·37	0·30	12·42
Cow - -	87·27	2·88	0·51	3·39	3·68	4·94	0·72	12·73
Cow colostrum -	75·07	4·19	12·99	17·18	3·97	2·28	1·53	24·93
Ass - -	90·12	0·79	1·06	1·85	1·37	6·19	0·47	9·88
Sheep -	83·57	4·17	0·98	5·15	6·18	4·17	0·93	16·43
Goat - -	86·88	2·87	0·89	3·76	4·07	4·64	0·85	13·12
Mare - -	90·58	1·30	0·75	2·05	1·14	5·87	0·36	9·42
Sow - -	83·94	—	—	7·23	4·55	3·23	1·05	16·06
Bitch - -	75·44	—	—	11·17	9·57	3·09	0·73	24·56

It will be observed that the milk of the sheep is rich in casein, but that of the dog contains the highest percentage of total protein, and likewise of fat, the sheep and pig coming next. The largest sugar content occurs in man, the next largest in the ass, which is closely followed by the horse. The highest amount of ash occurs in the pig, the lowest, next to man, being found in the horse.

The *Proteins* in milk are caseinogen, lactalbumin, and lactoglobulin. The latter contains phosphorus, and is probably a mixture of proteins. The proteins in milk are not precipitated by boiling; on the other hand, colostrum is precipitated; this is due to the presence of globulin.

Caseinogen is a phospho-protein, and the most important protein of milk; it occurs in a colloidal condition in combination with calcium, and is probably a mixture of several compounds, for it is not a clearly definite chemical substance (Heineman). Under the influence of rennin (p. 196) it is coagulated, forming a clot and whey, seen in curdled milk. The process is not fully understood, but the presence of calcium is necessary. The protein next in importance to casein is lactalbumin; it is allied to serum albumin, and is found to contain only a trace of phosphorus. Lactoglobulin contains phosphorus, and is probably identical with serum globulin. The origin of the lactalbumin and lactoglobulin is from similar bodies in the body fluids, but caseinogen has to be built up from the blood, and the manner in which it is constructed is at present unknown. The non-protein nitrogen in the milk of the cow is represented by amino-nitrogen and urea, both of which are increased on a high protein diet; there are also creatinine and creatine, but, according to Heineman, uric acid is absent. Hypoxanthine, xanthine, adenine, and guanine are present; hippuric acid is absent. The protein content of milk is liable to considerable variation, but is not so variable as that of fat.

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[*] ‘Milk,’ P. G. Heineman, Ph.D., 1919.

The *Carbohydrate* in milk is lactose or milk sugar; it is peculiar to the milk of all animals, and is not found elsewhere in the body, nor has it been found in plants. The table of analyses shows its proportion in the milk of different animals. Lactose readily undergoes fermentation, resulting in the production of lactic acid and the curdling of milk. The milk of the mare, cow, and camel, in the presence of suitable ferments, undergoes alcoholic fermentation, resulting in the production of koumiss and kephir. The source of lactose in milk is not decided upon; it is probably derived from the dextrose contained in the blood and food. Lactose is the least variable constituent in milk (see next paragraph).

The *Fat* in milk exists in the form of globules in suspension. It forms a true emulsion, each globule being separated by a layer of milk plasma. On standing, the globules rise to the surface of the fluid and form cream. This process can be much accelerated by centrifugalising the milk. By the process of churning the emulsion is destroyed and the fat obtained as butter. Butter consists of 68 per cent. palmatin and stearin, 30 per cent. of olein, and 2 per cent. specific butter fats (tributyrin and tricaproin). The source of the fat in milk is the fats and carbohydrates contained in the food. The question of its origin from the protein of the food has been greatly debated, and the point is not yet settled. The elaborate experiments of Jordan and Jenter suggest four sources of fat—the fat in the food, the body fat, protein, and carbohydrate. The most variable constituent of milk is the fat content; there may be 50 per cent. difference between the maximum and minimum; when the fat percentage is high the lactose is decreased. The differences observable in the composition of the milk solids are mainly dependent on the proportion of lactose to fat, though the percentage of these, taken together, is practically constant (Armsby). The first milk drawn is always poorer in fat than that obtained later. This is probably due to the secretion produced as the result of milking.

The *Salts* of milk are principally calcium phosphate, together with salts of sodium and potassium. The salts are derived from the blood and lymph, but do not exist in the proportions found in those fluids. Bunge has shown that the salts in milk are found in proportions closely agreeing with the requirements of the young animal. He compared the ash of a puppy with the ash of the milk of its mother, and the correspondence was remarkably close. On the other hand, the ash of the body of the calf, as determined by Lawes and Gilbert, does not agree with the mineral substances found in the milk of the cow, the calcium and phosphoric acid being twice those found in the milk. The iron also is very greatly deficient, but it has long been recognised that cow's milk is extremely poor in this metal (p. 780). On reference to the table of analyses striking differences will be observed in the ash content of the milk of various animals. The poorest in salts is that of the horse, the richest the pig's, followed by the milk of the sheep, dog, and cow. The rate at which the young grow can hardly be accepted as an explanation; it is also difficult to understand why the calf requires twice the amount of saline matter necessary to the foal.

The source of the salts in milk is the salts contained in the food. Nevertheless, a study of the ash metabolism of the cow shows very clearly that there are times when she is parting with more salts in the milk than she receives with her food. Even liberal feeding to the extent of a gain in body weight may not arrest this loss, and it is clear that the excess of salts in the milk over the ash content of the food can only be derived by the animal drawing upon the solid tissues of its own body. That the overdraft is made up in the later stages of lactation is probable, but Forbes, whose name is so closely identified with this work, considers that leguminous roughage or even bone meal should be given to prevent the loss. It was found experimentally that increasing the mineral content of the food was not sufficient; the repairing material is evidently required in organic combination. Cows fed on bone flour retain appreciable quantities of calcium and phosphoric acid, but wholly insufficient to maintain equilibrium or produce storage.* Forbes regards the depletion of the mineral reserves of the body as one of the factors in the natural shrinkage of milk production (Armsby). Cows, however, have been known to remain in milk for some years, as, for example, after the removal of the ovaries.

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* All recent observations connected with the mineral metabolism of the milch cow have been made in Experimental Stations in the U.S.A. It is well to note that experience in South Africa indicates that the phosphoric acid of bone flour is absorbed in sufficient quantities to control or prevent the onset of a disease of cattle which is induced by the animal's attempt to remedy a mineral deficiency. During the dry months of the year the

The drain on the system caused by the secretion of milk is considerable. Lawes and Gilbert published a table showing the weekly loss of nutrients as estimated by the content from various yields of milk. These animals were liberally fed, but the protein content of the ration, which the observers stated affected both the yield and richness of the milk, was not carried to the point of producing an increase in body weight.

BODY LOSSES WEEKLY.

Daily Yield of Milk.	Protein.	Fat.	Carbohydrate.	Ash.	Total Solid Matter.
	Pounds.	Pounds.	Pounds.	Pounds.	Pounds.
4 quarts	2·64	2·53	3·30	0·54	9·04
8 ,,	5·28	5·06	6·66	1·08	18·08
12 ,,	7·92	7·59	9·99	1·62	27·12
16 ,,	10·56	10·12	13·32	2·16	36·16
20 ,,	13·20	12·65	16·65	2·70	45·20

If an average secretion of milk be taken at 6 quarts (6·8 litres) per diem for forty weeks in the year, there is a loss of total solids equal to 542 pounds in weight, including 32 pounds of mineral substances; this is small compared with the loss in the deep milking strains of the present day, which produce 2,000 gallons, and even more, of milk in forty-four weeks, and yield half a ton of solid matter every year. These figures convey some idea of the metabolism occurring in the mammary glands and of their extraordinary powers of construction.

Colostrum.—This is the first milk secreted. It is a yellowish-white, sticky fluid, remarkable for the amount of protein it contains, which coagulates on boiling. Its analysis is shown in the table (p. 791). Not only is the protein content high, but also that of the ash; it is, however, poor in sugar. When examined microscopically, colostrum is found to be full of corpuscles, known as *colostrum corpuscles*, large granular bodies containing droplets of fat; they possess amœboid movements.

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grazing is insufficient to provide the needful phosphoric acid, and in consequence the cattle become bone-eaters. Putrid bones may be infected with a bacterium which elaborates a poison, or ptomaine, from the decomposing substance; this toxine produces a very fatal disease. If phosphorus be given in the form of wheat bran, as bone meal, or pure phosphoric acid, the craving for bones ceases. If the phosphorus be withdrawn the 'craving' returns (Sir A. Theiler, in the *Journal of Agriculture, South Africa*, June, 1920).

These cells are probably leucocytes; they are present immediately before and at the close of lactation; they may also be found during secretion if the glands be insufficiently 'stripped.' Normally the cells disappear from five to eight days after parturition, but even at this period the milk is not normal, for it is still acid, and it is not possible until the tenth day for the production of casein to occur. By the fourteenth day the milk may be regarded as of normal composition.

The function of colostrum is to act as a purgative to the young animal.

The **Yield of Milk** among cows is governed by various factors, of which, apart from food supply, the most important is the breed of animal. Milk production is essentially hereditary. Holsteins and Frisians hold the palm. On the authority of Alvord,* Shorthorns, Jerseys, Ayrshires, and Guernseys, are placed next in order of average milk production. Not only is quantity hereditary, but also the fat content. But there is no correlation between yield of milk and fat production; the Jersey is credited with the highest average percentage of fat. The influence of food on production is a commonplace.

Lawes and Gilbert regarded grass, and then swedes, as the best milk-producing substances in conjunction with the ordinary diet. In this protein is the most important constituent, for the food must contain not only the amount of protein contained in the milk, but also that required for the maintenance of the body (p. 393). Protein is believed to exercise a specific secretory effect over the mammary gland; further, it appears undoubted that the cow is able to utilise a larger percentage of the food protein for milk production than the ox can for beef production. At p. 399 is a brief statement of the daily calories required by a milch-cow under definite conditions of production. The amount of *assimilable* protein required in this case is at least 1·5 pounds per diem. Contrary to what might be expected, an increase of fat in the diet of cows above the standard of 0·5 pound of assimilable fat per 1,000 pounds of body weight does not lead to an increase in the fat of milk, though in sheep there is some evidence that it does assist. The physiological rule should, however, be that, short of increasing the body weight of a fully-grown animal, the rations cannot be too liberal. An increase in weight diminishes and eventually stops secretion. Underfeeding causes the percentage of fat in milk to rise and that of protein and ash to fall (Ekles and Palmer).

Galactagogues are agents which increase the production of milk. *Pituitrin* causes temporarily an increased flow, but it is not a galactagogue; it merely produces an increased flow by causing contraction of the walls of the milk ducts. On the other hand, extracts of placenta cause an increase in production. In women the extract produces an increase both in the protein and lactose; further, it is believed that a growth-promoting factor is also present which is passed on to the infant in the milk. All animals, the horse excepted, eat the placenta, and in cows it not infrequently produces impaction of the œsophagus. It is an instinctive habit which obtained no explanation until the galactagogue effects of placenta were discovered. Subcutaneous injection of the animal's own milk acts as a galactagogue; this is true of the woman and the cow, though in the latter the limited observations which have been made suggest that the increased secretion is only temporary. No drug can be relied upon to produce an increase of milk or butter. Castor oil decreases the butter fat (Forbes).

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* Heineman, *loc. cit.*

The natural galactagogue is sucking; this causes an increased secretion, and is the chief means by which the activity of the glands is maintained for months. 'Stripping' is the next best method; when imperfectly performed, the glands soon cease to secrete. Pressure on the gland also plays a part; the violent thrusts given by the lamb and other animals are a secretory excitant.

Secretion soon ceases if the glands be not emptied, and atropine, or its preparations, also causes it to stop.

The average duration of lactation in the cow is about forty weeks in the year; as previously noted, if ovariotomy be performed when in full milk, the secretion may be maintained for two or three years, some say even longer. Cows have been known to remain in milk for five years after the last visit to the bull (H. Gray). Gestation may hasten the close of lactation, but it does not influence the composition of the milk until towards the end of lactation, when an increase in protein and fat occurs, and frequently a decrease in lactose (Palmer and Eckles). As a rule, the greatest flow of milk occurs within two or three weeks after parturition, and then it gradually becomes reduced as the next period of gestation approaches, but there are marked individual differences.

SECTION 3.*

Heredity.

As no living thing arises spontaneously, but is built up from a pair of other living things (with certain exceptions in the simpler forms of life), it is probable that so long as man has been able to reason he has regarded the offspring of a given union as consisting of a mixture of its parents. As knowledge became extended, more especially since the origin of species has been traced almost step by step from the lowest to the highest forms of life, and all life shown to be the outcome of a common primitive form, the facts underlying these extraordinary changes have been the subject of inquiry, in order to determine the natural laws by which they are governed.

The terms 'evolution' and 'origin of species' have become so closely associated with the name of Charles Darwin that it is apt to be forgotten that the idea of a common descent for all living things had been prominent in the minds of naturalists long before Darwin's day.

The French scientist, Lamarck, and Darwin's grandfather, Erasmus Darwin, though they did not originate the idea of a common origin, formulated the theory that evolution was due to the transmissibility of modifications acquired during the lifetime of the individual. This parental experience might be positive or negative. In the former case the result took the form of increase in size and function of the parts or organs concerned. On the other hand, Lamarck maintained that the continued lack of use of the same organ sensibly weakened it, leading to deterioration and ultimate disappearance.

In order to account for the stability in the filial generations of parental reaction to environment and parental experience, Lamarck held that Nature preserved everything that she had caused the individual to acquire or to lose by the influence of the circumstances to which the race had been for a long time exposed, and consequently she preserved everything acquired by the predominant use of certain organs (or lost by their continued disuse). She did this by the generation of new individuals, which were produced with the newly acquired organs. This occurred, provided that the acquired changes were common to the two sexes, or to the individuals that produced the new forms.

The Lamarckian position is still very strongly held, especially in France and America, but as pointed out by Professor E. Ray Lankester, Lamarck's laws are contradictory. In the first place, he inferred that old characters had not become fixed and congenital after a multitude of successive generations had developed them in response to environment, but gave place to new characters when new conditions operated on the individual. Why, therefore, should we conclude that new characters are likely to become fixed after a relatively shorter time of responsive existence ?

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* This section has been revised by Mr. J. B. Robertson, M.R.C.V.S. The author takes this opportunity of expressing his indebtedness to Mr. Robertson for the revision and for his many communications and guidance on the subject of heredity.

Charles Darwin's views on the Lamarckian theories varied somewhat from time to time. In his 'Origin of Species' he held that heredity and adaptation enter into close reciprocal action. In the struggle for existence, only those individuals survived which were naturally selected by their environment, and this selection, Darwin contended, took place through the medium of impalpable differences and through the course of a long period of time. In other words, owing to the removal of the least fit, selection took place through the most fit—*i.e.*, most fit for the conditions in which the organism existed. This theory of the survival of the most fit was the central difference between Darwin's conception of evolution and the views of Lamarck, for both believed that somatic acquirements were the fountain-head of corresponding modifications in the germ plasm, and also that Nature did not make 'jumps.' But extended investigation has shown that 'jumps' are occasionally made. Indeed, it is difficult to account for the multitude of specific forms which now inhabit the earth, or for pre-existing forms which have inhabited it and become extinct, if we accept the theory that evolution is brought about solely through the medium of small modifications.

Weismann, in his work on 'The Continuity of the Germ Plasm,' advanced the opinion that only those characters could be transmitted to subsequent generations that were contained in rudimentary form in embryonic tissue. Variation in effect commenced in the germ plasm, and not, as postulated by Lamarck and Darwin, in the soma. Weismann consequently very strenuously opposed the doctrine that parental somatic experience was ever transmitted. The germ plasm, he pointed out, is continued from generation to generation, but is subject to inborn transformation, and the environment through its finished product, the soma, selects the fittest or most suitable plasm, the modification so selected being thus transmitted to the germ plasm of the next generation. A clear conception of the two theories is of paramount importance to the student of heredity. We shall see presently that the consensus of present opinion is against the transmission of purely somatic acquirements. Only those characters which are innate, and therefore the outcome of germinal determinants, are transmissible.

The *mutation theory* of de Vries was also in sharp contrast to the fundamental principle of Darwinism, which laid down the central idea that changes were extremely slow and gradual. According to de Vries, no new species can be established without mutation. 'When a mutation has occurred a new species is already in existence, and will remain in existence, unless all the progeny of the mutation are destroyed. . . .' The phrase 'survival of the fittest,' as describing a process of evolution, ought, de Vries contended, to be replaced by survival of the fittest species. . . . Natural selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest.' De Vries, in his first essay, was a remarkable pioneer in the conception of unit characters which are so intimately associated with the name of Mendel, and in his second he very clearly pointed out the marked distinction between fluctuating variations and true genetic variations, or mutations. Each mutation, he contended, is the centre of a group of fluctuating variations, and unless there be very rigorous selection, fluctuations do not lead to a permanent change in the mean of the species, and even then, if the selection be slackened, there is a regression to the old mean.

It has been asserted that the mutation theory of de Vries has been amply verified in plants, but that it cannot be applied with certainty to the animal kingdom. The development of the British thoroughbred horse during at least the last two hundred years is a clear proof of the fallacy of the latter contention. The truly phenomenal strides made by him in physique, speed, and racing stamina could not possibly have been effected through the operation of fluctuating variations on the twenty odd filial generations which separate him from his ancestors the Arab, Barb, and native English racing Galloway. From time to time mutants have arisen which have served as the parents of the race, and very appreciably raised the mean capacity in the all-important characters which make for success on the turf.

What has been said of the impregnation of the ovum (p. 762) is sufficient evidence that both parents contribute in an equal degree to the construction of the offspring, and there is not much difficulty in conceiving that not only the parents concerned, but their ancestors, are represented, though in ever-diminishing degrees. An animal or plant is therefore a mixture of its ancestors, and the question whether in this complex the individual characteristics remain distinct, or whether they are blended, is one which during the last few years has received the closest attention. If they are blended, modifications in various directions may in consequence arise; if they are not blended, variation must be ascribed to the introduction of a new unit character or characters by one of the parents, or alternatively to a character which had been carried in a state of latency becoming patent. A blending of certain characters in the soma is not denied by the Mendelists, but they hold that, as there is no blend of character determinants in the germ plasm, the somatic blend is not transmitted as such to the filial generation.

Galtonism.—That an individual is a mixture of its parents and their progenitors is but a bare statement of the law of heredity with which the name of Galton will ever be associated. As the result of his careful inquiries and elaborate statistical data on stature and other qualities in man, and on coat colour in basset hounds, Galton formulated his law of ancestral inheritance, which he stated as follows: 'The two parents between them contribute *on the average* one-half of each inherited faculty, each of them contributing one-quarter of it. The four grandparents contribute among them one-quarter, or each of them one-sixteenth, and so on, the sum of the series $\frac{1}{2}+\frac{1}{4}+\frac{1}{8}+\frac{1}{16}+\ldots$ being equal to 1, as it should be. The bias towards particular diseases, or tendencies to such diseases, conveyed by any particular ancestor in any given pedigree tends to be eliminated by a law which deals only with average contributions, and the various prepotencies of sex in respect to different qualities, such as the familiar sex-limited diseases of pseudo-hypertrophic muscular paralysis, hæmophilia, and colour-blindness, are also presumably eliminated.' The essential feature to be borne in mind in connection with Galton's law is that it applies to masses rather than to the individual. It is an average result, the immediate parents in all cases being, on the whole, more largely represented than any of the other progenitors. For the improvement of a breed it is essential, according to Galtonism, that the laws of artificial selection should prevail. These, acting over a sufficient length of time, would blend in desirable proportions the special qualities required in the mass, though they might be absent in the individual. In further explanation it is necessary to add that the whole of the parental and ancestral contributions transmitted to the offspring must be represented in the germ plasm of the parents. The parental share in the offspring's inherited faculties refers to the outward, visible, demonstrable characters present in the parents, and not to their latent characteristics.

Although, as already stated, the law of ancestral inheritance is more applicable to the family group than to the individual, nevertheless it is of very considerable assistance in working out the probable filial capacity resulting from a given mating, provided always that the ancestral capacity in the trait or quality concerned is accurately known. And ancestral capacity here applies not only to somatic capacity, but also to reproductive capacity.

Mendelism.—The latest view of heredity is that put forward by Mendel many years ago, though it remained unrecognised until 1901. It is difficult to define it in precise terms until examined, but it aims at applying physiological laws of inheritance to the individual rather than to the mass. It does not at present, and may never be able to, deal with all the characteristics of individuals. In the case of the more important faculties in man and animals the application of Mendelian principles is as yet somewhat limited. Mendelian inheritance is known to exist in the matter of coat colour and length of fur in rabbits, and of the fleece in sheep. It applies to the coat of various breeds of dogs—*e.g.*, fox hounds, basset hounds, and terriers. It also applies to eye colour. In the case of cattle and sheep it applies to coat colour and horns, and in dairy stock, it is said, to the quantity and quality of milk.* In poultry, to plumage, combs, feathered or clean legs, and extra toes, as opposed to the normal condition. In the horse it applies to coat colour, and, as Robertson† has shown, to 'staying' power, to the number of lumbar vertebræ, to the shape of the nasal bones, and to the shape of the ears in the race-horse, and in Shetland ponies to hock callosities. The principles apply much further in the case of plants, dealing with such features as height, characters of flowering-head, leaves, and stem, and have already been turned to useful economic account in husbandry by the production of new and improved species. The characters spoken of above are described in Mendelian phraseology as **Unit Characters.**

The union of the ovum and sperm cell and their subsequent division, described at p. 761, enables the essential facts of Mendelism to be visualised. In Mendelian terminology either generative cell is spoken of as a **Gamete,** and the organism resulting from the union of two gametes is called a **Zygote.** We have seen that each gamete contains half the number of chromosomes found in the body cells, so that when the zygote is formed it is a double structure consisting of an equal contribution of chromosomes from each parental gamete. The resulting plant or animal retains in its cells throughout life the double structure imparted by the two complete sets of chromosomes, one derived from the father, the other from the mother. As was stated on p. 755, the inheritance of characters is believed to be connected with the chromosomes.

Each chromosome contains within it the hereditary factors arranged, it is suggested, end to end like beads on a string. Each factor corresponds to a characteristic in the animal from which it has been derived—eye and coat colour, height, body-build, temper, disposition, sex, longevity, instinct, milking capacity, early maturity, horn production, constitutional vigour, speed, stamina, fertility, and the scores of features which distinguish animals of the same class from each other. All the factors are not necessarily transmitted to the offspring, but where they are alike in the parents the chances of their transmission are enormously increased, and some factors are reproduced with certainty. This is the principle of in-breeding. The offspring is a complex of the factors derived from both parents, the whole being rearranged in the chromosomes of the new animal. The number of new arrangements possible in the paired chromosomes of the horse amount to nearly sixty-nine millions, so that some notion may be formed of the capacity which exists for variation. Fortunately, from an animal-breeding point of view, the factors carried by the parental chromosomes may be linked together in groups, though the linkage is elastic, and consequently tend to be inherited in groups.

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* Professor J. Wilson, M.A., *Proceedings of the Royal Dublin Society,* 1910-11.

† See footnote, p. 438.

We have seen that the cells in the living organism are divided into two groups—body or *somatic*, and reproductive or *germ cells* (p. 751). The absence of blending referred to on p. 799 refers solely to the generative cells. The soma, or body, is the envelope containing the generative cells, and between one generation and another there is no continuity in the cells of the soma. The link between generations lies in the germ cells. It is generally conceded that environmental conditions may modify the somatic cells of the individual, but that they exert no appreciable influence on the generative cells. Modification of the somatic cells not being heritable, it is to the influence of natural selection transmitted through the generative cells that variations must be attributed.

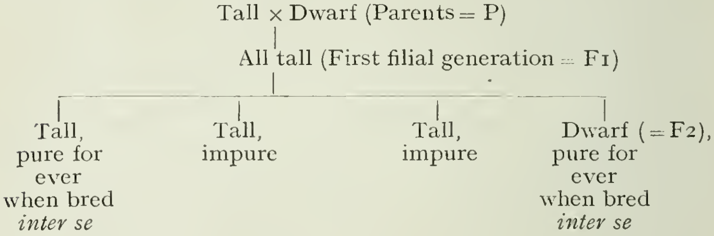
When a pair of zygotes breeds true for any given unit character, their gametes must in respect of that character be identical, and the resulting offspring of their union carries in its generative cells the same unit character. When two zygotes are mated which breed true for *opposite* unit characters, such as tallness and shortness in the common pea, the gametes produced by each, for the particular unit character of height, are not identical, but opposite. The resulting offspring in the *first* generation are not, however, in the matter of height, a mixture of the two zygotes; they take after one parent or the other, not after both, and whichever characteristic they follow is the **dominant** one; that which the body cells have not followed is the **recessive.**

But though the body, or somatic, cells of the offspring have followed the characteristic of either one or the other parent, their generative cells are a mixture of the unit characters of both. In spite of being mixed, there is no blending; the cells producing tall do not fuse with the cells producing short plants, and subsequently result in those of medium size. The **determinant** or **factor** which produces tallness and the determinant or factor producing shortness, though both present in the generative cells of the zygote, are as clearly and sharply separated as if only one factor were present. When subsequently this zygote produces a generation, it will be found that half its gametes carry the factor for tallness and half carry that for shortness. This unblending or separation of the cells is described as **Segregation.** A single gamete must, in this way, be pure for either one or the other of two opposite characteristics; in the example selected it must be pure for tallness or pure for shortness, inasmuch as we have seen that no blend of the two is possible.

The whole Mendelian structure pivots on the segregation of characters as outlined above, and the purity of the cells forming the gamete.

Mendel's work was done on the common pea, and the essential facts are known in this plant with the greatest precision.

Selecting shortness and tallness from among several pairs of contrasting characters which the pea furnishes, Mendel found, on crossing a pure tall with a pure dwarf, that the offspring, or first generation, were all tall. This settled that in the pea tallness is *dominant* and shortness *recessive.* If the first generation be self-fertilised, a second generation is obtained. These are no longer all tall; there are some short, and the proportion of tall to short plants is as three to one. The dwarfs of this generation, if bred among themselves, never produce anything but dwarfs, and so on in every succeeding generation. The dwarfs, we have seen, are recessive, and in Mendelian phraseology recessives breed true. The three talls of the second generation, if bred among themselves, behave as follows: One will produce all tall plants, and continue to do so to infinity; the remaining two talls behave differently. They do not breed true, but each produces in a next generation talls and dwarfs in the proportion of three talls to one dwarf. Of these, one tall and one dwarf breed true, while two talls are impure. These facts are shown in the following table:


Tall × Dwarf (Parents = P)
All tall (First filial generation = F1)
Tall, pure for ever when bred *inter se*
Tall, impure
Tall, impure
Dwarf (= F2), pure for ever when bred *inter se*

Reviewing the above classical example, it will be seen that the first generation, though all tall, contained in the generative, as apart from the body cells, the factors both for tallness and shortness. There was nothing in the appearance of these tall plants to indicate that they differed from their tall parent, or that they carried a recessive character segregated, but it became evident in the second generation that three different plants existed—viz., a true tall, a true short, and an impure tall. In the third generation it was shown that the pure tall and pure short bred true, and that the impure tall bred pure talls, impure talls, and dwarfs, in the proportion of three talls or dominants to one short or recessive.

The above example illustrates the simplest form of Mendelian inheritance, and Mendel showed that each of the seven pairs of contrasting characters found in the common pea behaved in the same way—viz., for each of the distinguishing characteristics the dominant was to the recessive as three to one in the second filial generation, F2.

Examples of the Mendelian law in the breeding of animals are less numerous than in the case of plants. If, however, pure polled cattle are crossed with pure horned cattle, the resulting generations behave precisely as in the contrasting characteristics of the sweet pea. The first generation will all be horned. If the first generation be interbred the horned and polled factors separate out in the second generation; one-quarter will be pure polled, one-quarter will be pure horned, and half will be hybrids. There is nothing in the appearance of the hybrids to distinguish them from horned cattle, but if bred to other hybrid cattle they will produce one-quarter pure polled, one-quarter pure horned, and one-half hybrids. A pure horned or a pure polled breed may thus become established. Difficulty is encountered in determining the hybrids, as these carry horns; the hybrids can only be ascertained by the production of further generations.

Dominance has been illustrated by the above recorded experiments, in which it has been seen that the resulting zygote is a pure dominant when both gametes are pure for the particular character, and impure when only one gamete imparts the dominant variety. There is no difference in appearance between the pure and impure dominant above mentioned, but the test of breeding from them at once settles the question. In some cases a zygote differs from either parent by being intermediate in size or by physiological properties, but the offspring of two such zygotes follow the ordinary Mendelian law—viz., they reproduce the parental and the intermediate characteristics in the second generation. The parental characteristics in the next generation breed true; the intermediates behave as in the first generation—in fact, in accordance with the classical illustration of the peas. In such cases dominance is absent, and it is usual to state the fact by saying that dominance is not a necessary feature of Mendelian inheritance.

The following are examples of dominance in animals:

Bay, brown, and black dominant to chestnut in horses
Grey dominant to black in rabbits and mice.
Black dominant to white plumage in fowls (in certain breeds).
Polled dominant to horns in cattle.
Short coat dominant to long coat in rabbits, sheep, and dogs.
Feathered legs dominant to clean legs in poultry.
Extra toe dominant to normal condition in poultry.
Six lumbar vertebræ dominant to five lumbar in the horse.
Convex nasal bones dominant to concave in the horse.
Melanism dominant to albinism in all animals.

The inhibitory factor to which greyness in horses is due is dominant to its absence.

No explanation can at present be offered why dominance is present in one case, absent in another, and irregular in a third. In the following example of irregular dominance in sheep it is supposed that sex is the determining cause: Dorset horned and Suffolk hornless sheep were crossed, and the first generation resulted in the rams being horned and the ewes hornless. Bred among themselves, the several generations produced rams of which only three-fourths were horned, and ewes of which one-quarter bore horns. In this case horns or their absence depended upon sex, horns being dominant in the ram and recessive in the ewe. This was proved by mating a hornless ram with the hornless ewes of the first generation, the resulting progeny showing that half the rams were hornless and all the ewes.

Only an outline of Mendelism has been sketched above, and nothing but its simpler side explained. When applied to many cases of inheritance, Mendelism is not found to behave with the simplicity above indicated. For instance, it is no longer considered necessary to assume the existence of two factors to represent contrasting characters. Tallness or shortness in the pea is not due to a factor for tallness and another for shortness, but to one factor in two possible conditions—*i.e.*, *present* or *absent*. If present, the pea is tall; if absent, it is short. Two or more distinct factors in the gamete may also act on each other, and so influence the resulting zygote. This is known as the *interaction of factors*, and is a question of supreme importance to the Mendelist. Factors may also repel or attract one another; this is the theory designated the *repulsion and coupling of factors*. These are mentioned in order to illustrate some of the difficulties and complexities of the doctrine; the consideration of these is beyond the scope of this work, and requires expert treatment.

Evolution.—It is natural that Mendelism should be searched for an explanation of the evolution of the domestic from the original wild species. It is suggested by those to whose opinion great weight is attached* that the addition of factors, the subtraction, or the interpolation of factors will explain the little which is clearly known of evolution. For instance, there appears to be no doubt that the present sweet-pea in its many varieties arose from the wild sweet-pea introduced into this country a little more than two hundred years ago.† In this case the numerous present-day varieties have arisen, as is supposed, by the subtraction of factors. All the necessary elements for the production of the many civilised varieties are believed to have existed in the wild plant, but one by one those inimical to their production have been eliminated. The Mendelist does not reject the influence of variation, but he attaches to it a far stricter interpretation; he does not believe that variation need necessarily be small in amount, nor require ages to become adapted, for it can be shown that marked variations, known as '*sports*,' may appear in a single generation. He further recognises two forms of variation: the one which may appear quite suddenly, and is transmissible by the gametes, since it is due to the existence of 'factors'; and the other which is acquired in consequence of the conditions of life under which the organism is living. The first has been called *mutation*, and has already been referred to; the second is *somatic fluctuation*, and, not being represented in the gametes, is consequently not transmissible. The process of evolution depends upon mutations, and natural selection determines whether their continued production shall be maintained or rejected. It is stated by Punnett‡ that a rare 'sport' with 5 per cent. selection in its favour will replace the normal in a few hundred generations. This being so, evolution generally demands a far shorter time for its production than has generally been supposed, and no better evidence of this can be brought forward than the improvement, based on artificial selection, of the breeds of domesticated animals within recent generations.§

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* 'Mendelism,' R. C. Punnett, M.A., third edition, 1911.

† *Op. cit.* ‡ *Op. cit.*

§ In the matter of the race-horse, certain exact data are available for a considerable period, and the bearing of Mendelian inheritance on this animal has formed the subject of special study. See 'The Principles of Heredity applied to the Race-Horse,' by J. B. Robertson, M.R.C.V.S., 1910.

Mendelism is still in its infancy, and its application to the breeding of the larger stock, excluding poultry, has been determined only to the extent recorded at p. 803. There are difficulties in obtaining in animals the results readily effected in plants. One of these is that the sexes have to be provided by two distinct physiological units which may differ widely from each other, whereas in those plants which are produced by self-fertilisation the constitution of the male and female elements is identical.

The laws of inheritance of such unit characters as coat and eye colour are known with considerable precision. The whole trend of the work on heredity from the time of Darwin onwards has shown that it has a physiological basis, and when regard is had to this fact, even though the breeder is, as has hitherto been the case, working in the dark, results of the highest economic importance have been obtained. It is not too much to hope that the great precision given to heredity by Mendelism will in time replace the policy of 'hit or miss' by something approaching exactitude. Already it has explained, through the simple term 'recessive,' the previously incomprehensible fact that a character may 'skip a generation'; it also offers an explanation of *reversion** and *atavism.*†

Telegony is the supposed influence of a male by whom a female has previously conceived on her subsequent offspring by another male. For generations this supposed influence was the dread of breeders. It possessed no physiological explanation, and was finally conclusively shown by Cossar Ewart to be without a shadow of foundation (see also p. 783).

Heredity in Disease.—Of the influence of heredity in disease there is no possibility for doubt. Arrested development of the fingers in man, night-blindness, colour-blindness, hæmophilia, and a few other conditions, have been shown from constructed pedigrees to follow, or closely approximate to, the laws of Mendelian inheritance. So far as the hereditary diseases of animals are concerned, their Mendelian examination has barely begun, and in the very nature of things must take a long time to accomplish. Robertson has shown, from his inquiry into 'Roaring and Ruptured Bloodvessels in Race-Horses,'‡ the possibilities awaiting patient investigations. On the question of the inheritance of disease considerable caution is necessary. There are few veterinary practitioners with experience of stock-breeding who are not impressed by the hereditary nature of such diseases as bone-spavin, ring-bone, side-bone, 'shivering,' springhalt, cataract, and navicular disease.

It may be that our ideas concerning the actual nature of the transmitted characters which lead to some, if not all, of the above conditions will have to be modified. Chemical composition, or even molecular arrangement, may ultimately turn out to be the determining factor. No biologist would, for instance, assert that bone-spavin was represented by a unit character, but he would accept the view that some particular condition of hock articular cartilage led to bone-spavin. He would also admit that this specific cartilaginous condition might well be represented by a determining unit character, and that this character passed from parent to offspring. In these circumstances it is conceivable that bone-spavin due to a defect or modification in the germ plasm would be heritable. On the other hand, if arising from sprain or trauma, its heredity would be absent, for somatic acquirements are not transmissible (Robertson).

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* A return to some type of ancestral character, as when a black and a white rabbit produce a grey, which is the colour of the wild form. Chestnut is a reversionary character in the horse (Robertson).

† 'Throwing back,' or atavism, is the appearance of ancestral racial characteristics, as, for example, the extra digit sometimes found in the horse.

‡ *Op. cit.*

Robertson's investigations have shown that roaring, side-bone, 'shivering,' and a tendency to ruptured bloodvessel, follow the laws of Mendelian inheritance.

SECTION 4.

Breeding.

By J. B. ROBERTSON, M.R.C.V.S.

These islands have for many centuries been famous for their flocks and herds, but little progress was made in the improvement of breeds until the middle of the eighteenth century. The explanation is that the open field and land-in-common system of farming, which prevailed until the close of the seventeenth century, gave no opportunity to create improved sub-varieties; further, the methods of farming were backward, little or no provision being made for winter keep, so that the stock emerged from the stress of winter in a state of semi-starvation.

When the production of turnips, clover, and artificial grass was rendered possible by the work of J. Tull and of Viscount Townshend, the middle of the eighteenth century showed a vast improvement in the winter provision of food for stock, concurrently with an all-the-year-round supply of fresh meat for the industrial population in place of the salted food they had previously obtained.

Then came R. Bakewell (1725-95), a farmer and grazier of extraordinarily advanced views, both on agriculture and breeding. He determined to create improved breeds of sheep and cattle, and at the same time to increase the output of meat. He succeeded, not by any haphazard methods, but by the rigid use of experimental inquiry; his Leicester sheep were the best in the world, and were in demand even as far off as America. His long-horn herd of cattle became equally famous. Bakewell's methods were the careful selection of original stock, and the obliteration of all progeny which did not come up to his standard. He established a museum in which were kept the skeletons and soft parts of his various experimental animals, so that a comparison could readily be made to test his progress. He also adopted the principle of in-breeding. In this respect Bakewell was not original. Even as far back as the time of the Stuarts in-breeding had been employed for the racing Galloways of the northern counties of England, also for hounds, and doubtless for fighting game-birds. Bakewell applied the same methods to obtain improved sheep, cattle, and horses for agricultural purposes. In respect of the latter, he had the object-lesson afforded by Leedes of Yorkshire, who, forty years before Bakewell was born, had produced by in-breeding two horses, Cream Cheeks and Fox, whose names are repeated many hundreds of times in the pedigree of every thoroughbred horse in the world. The difference, however, between the methods of Bakewell and of those who preceded him in in-breeding is that, whereas in the case of horses, hounds, and game-fowl their performance had been the test, Bakewell worked on the method of purely artificial selection, guided by his extraordinary judgment, so that his progress was relatively rapid. One of his rules was this, that the male parent was the more important of the two in racial improvement. He selected, for early maturity, thick flesh, light offal, and fair milking qualities in his cattle, early maturity and wool in the case of sheep. It must be remembered that Bakewell could have done nothing but for his improved system of agriculture; his farm became the Mecca of agricultural students, both at home and abroad. His pupils carried his practice far and wide; two of the earliest and most distinguished were the brothers Colling, both excellent judges of cattle, who subsequently founded the modern Shorthorn breed. Among their contemporaries were T. Bates (1776-1849) and T. Booth, who, drawing on the Colling herds for stock, revolutionised stock-breeding, particularly in Ireland and South America, while the Dairy Shorthorns of Bates furnished the female 'tap-roots' of many of the best strains of the present day. Certain stocks, such as the Channel Island cattle and the Kerries of the south-west of Ireland, were of purer origin than the modern Shorthorn, and in consequence did not furnish so much scope for the breeder's art.

The principle of in-breeding applied to the improvement of cattle and sheep has since the days of Bakewell been applied to horses other than thoroughbreds, but the resultant improvement is based on show-ring standards and has not proved an unmixed blessing. Certain of the 'fancier' points relating to the Shire, Clydesdale, Suffolk Punch, Cleveland Bay, and Hackney are far from being correlated with ability to excel in heavy and light draught work. The long sloping pasterns, large spreading feet, and inturned hocks of the Clydesdale are considered the acme of perfection by his admirers, yet these characteristics are viewed as the worst possible defects in the Shire or Suffolk Punch. In like manner the coarse integument and long hair on the limbs of the Shire have been carried to such a point as to predispose him to pathological conditions such as coronitis, lymphangitis, and 'grease.'

All the horse stocks of the world are referable to three species of Equidæ—viz., *E. robustus*, *E. przewalskii*, and *E. agilis*. The Shire horse of the present day presents all the characteristics of *E. robustus*. and, being pure, he breeds true to type, the biggest, coarsest, heaviest, and most hairy-legged variants being unfortunately selected as breeding units. *E. przewalskii* and *E. robustus* are combined in the Suffolk Punch, Clydesdale, and Percheron. *E. robustus* and *E. agilis* are found in the Cleveland Bay and Hackney. The modern representatives of *E. agilis* are the Arab, Barb, British Thoroughbred, and a few Celtic ponies. It hybridises with other species, but permanent sub-types can only be evolved with the greatest dffiiculty. Failure to recognise this is the explanation of the many mis-shapen animals included in the category of light horses. Individuals of the second filial generation, when bred *inter se*, show marked segregation, but not on specific lines, so that in the third and fourth parental generations variations of an undesirable character are frequent. It is also well established that the thoroughbred stallion is considerably less fertile with common mares than with mares of his own species. The ignorance exhibited by the agriculturists of England and Scotland in putting any degenerate specimens of *E. robustus* to the thoroughbred horse shows the condition in which the breeding of half-bred horses is at the present day. The farmers in the south of Ireland have made fewer mistakes, for the reason that the mares at their command have in the distant past sprung from a stock saturated with the blood of the thoroughbred, directly or indirectly. To mate these mares with the Clydesdale and Shire, as has been done in recent years, shows the ignorance which exists of the physiology of breeding.

Knowledge of the physiology of breeding has of late years been considerably augmented by the Mendelian theory, and by cytological evidence. Our conception of the pure-bred thing is no longer vague, but clear-cut and definite.

Formerly it was believed that persistent saturation of several generations was necessary for the fixation of a character, and that this had to take place before a male or female could become 'prepotent' as a parent in a particular attribute. We now know that this was erroneous. All that is necessary is that a chromosome in the nucleus of the spermatozoon and a chromosome in the nucleus of the ovum shall bear chromatin granules which are alike in respect of the particular character desired. Hence 'prepotency,' or the power to stamp parental character on the soma of the offspring, is not correlated to length of ancestry, but is governed by clearly definite rules, now styled *dominance* (see p. 803).

The thoroughbred's ancestry has been known for upwards of 200 years. He is the product in all cases of an exceedingly small number of individual ancestors, and is the most intensely interbred domesticated animal in the world. The parents of the breed are selected by the race-course test, which picks out the plus variants in speed, stamina, and ability to stand the severity of training. It is generally accepted that the distribution of the paternal and maternal chromosomes to the gametes of the filial generation is entirely a matter of chance. On the basis of eighteen chromosomes in the mature reproductive cell, the number of combinations possible in the gametes are 262,144, and in the zygotes 68,719,476,786. These figures give some idea of the capacity which exists for variation. The chance of producing desired combinations are increased by in-breeding with animals possessing the desired correlations.

The extent to which in-breeding may be carried with safety depends on the degree in which the race generally has been interbred. When the parents of the first generation are in no way related, in-breeding may be carried to extreme lengths in the succeeding generations without harmful consequences. As already pointed out, the thoroughbred has been intensely interbred, no new blood having been introduced for practically 200 years. In place of having the full complement of 16,384 individual ancestors in the fourteenth parental generation, no modern thoroughbred has more than fifty, and many have fewer than that number. In the tenth and twelfth generation the number of male ancestors is reduced to three, and of these three Eclipse enormously predominates. In consequence, it is not possible to find thoroughbred horses which are not related in blood.

In the racehorse and greyhound the methods by which the parental generations are selected—namely, their performance—tends automatically to keep a sharp check on too close in-breeding, for the degenerates have no chance of becoming racial parents.

Similarly, dairy stock is selected by the capacity to produce deep milkers. Cattle and sheep are judged by the early maturity they attain. Elimination is carried out by the judgment of the breeder. Bakewell, Bates, the Collings, and others did not hesitate to sacrifice any animal not coming up to their standard, and to this may be attributed the fact that the introduction of new blood was a matter of rarity. Bates used no new blood for the first thirteen years; during the next seventeen years he introduced it three times, always on account of a reduction in fertility, which is the most obvious and the most frequent indication of deterioration. Price, a breeder, stated in 1841 that his cattle had been closely in-bred for eighty years without fresh blood. As surely as good qualities are transmitted by in-breeding, so are heritable diseased conditions intensified (see p. 805).

The characteristics transmitted to the offspring by each parent have been a subject of fruitful speculation among men of equally wide experience. The liability to variation where the parents are not of fixed type and the prepotency shown by either the male or female in stamping its likeness on the progeny are two factors which must always influence the tranmsission of characteristics. The broad rule more or less generally accepted by breeders is that the male parent influences the external structures, vigour, courage, and organs of locomotion, while the female transmits the internal organisation, temperament, and organs of nutrition. Physiologically it seems impossible to accept this, though if we regard the mule as a test case the rule appears to apply. In this animal we have the offspring of two widely contrasting parents, with the result that the male, the ass, is strongly represented in the external structure and organs of locomotion. When the male parent is the horse, the resulting 'jennet' partakes of the appearance of the horse so closely that at first sight it might pass as a pony.

The careless manner in which the public discuss the practice of breeding shows the remarkable ignorance which exists of this most complex of all physiological phenomena. There is no branch of industry which requires so long an apprenticeship, and this even is of no avail without the 'breeder's eye,' a gift which few men possess.

CHAPTER XIX

GROWTH, DECAY, AND DEATH

Growth.—This subject has already received some consideration in dealing with nutrition (pp. 368, 376); it was referred to in connection with vitamines (p. 390), and at pp. 305, 306, and 307 isolated references had been made to the influences on growth exercised by certain endocrine glands.

We have seen that the growth impulse is most pronounced in intra-uterine life, and is diminished from birth to maturity, at first rapidly, then slowly. During fœtal life the production of new tissues is the characteristic feature of growth. Broadly speaking, in extra-uterine life no new tissues are produced by the herbivora; the existing tissues are developed by cell multiplication, but especially by an increase in cell contents and intracellular material. Growth cannot be explained as resulting from an increase in the size of the body cells, for their limits are fixed. The energy of intra-uterine metabolism in the herbivora is devoted to the production of protein and inorganic tissues to enable these animals to move freely at birth without undergoing the period of helplessness so prominent in man and the carnivora. To this end the bones and muscles are rendered capable of playing their part as organs of locomotion from the moment of birth. The store of fat, so well seen in the subcutaneous deposits in the human infant, is entirely absent in new-born herbivora.

With the carnivora the intra-uterine development is incomplete, and new tissues continue to be produced after birth; for example, the eyes of the puppy are not completed for vision until the fourteenth day after birth, and it is not until the thirty-fourth that a dog avoids obstacles. Similarly, the locomotor apparatus is incomplete at birth, and further development has to take place before standing and walking are possible.

The importance of protein in the food of the young growing animal has already been dealt with, also the remarkably complete manner in which it is utilised by the herbivora. It is this which leads to the deposition of protein in the body, and the facility with which the protein accumulates has been taken advantage of in the production of early beef and mutton maturity, which has long been recognised as the basis of economical meat production. As the animal grows older the tendency to store up protein is diminished, nor can it be stimulated by increasing the amount in the diet.

The increase in weight of very young animals is largely water; as much as 80 per cent. of the gain may be so represented, but as early maturity approaches the water gained by the tissues becomes less and less, and finally drops to 30 or 40 per cent. of the gain. The storage of dry matter in the very young is, as we have seen, largely protein, while as early maturity approaches the increase in weight is largely fat with some protein. The storage of salts is very high, especially in the young while still suckling, and gradually diminishes, though not so rapidly as does that of the organic substances, (see p. 385, where a table is given showing the retention of salts in the body).

We have seen that the young of the herbivora very rapidly shake off the helpless condition in which they first find themselves in this world. This is largely due to the fact that they are born with a nervous and locomotor system in a high state of development; in the course of an hour or less they learn to stand and walk, and in a day or two can skip and run. The young animal, moreover, is born in full possession of its senses, such as sight, touch, hearing, smell, taste, and with an amount of intelligence which nearly, if not quite, equals that of its parents. It has practically nothing to learn but obedience to man. The legs of the foal are remarkably long, some of the bones being nearly their full length (see table, p. 813), though, of course, not their full weight; such joints as the knee and hock have very little to grow. We can understand the reason of this development of the limb from what has been said above, while the length of leg in the foal is undoubtedly for the purpose of enabling the animal to reach the mammary gland. The limb, however, is only partially developed; from the knee and hock to the ground it is nearly the same length as in the adult; from the knee to the elbow and the hock to the stifle it is decidedly below the adult, whilst from the elbow to the withers, and the stifle to the croup, the body has a considerable amount to grow. It has been said, and the statement appears to be true, that the future height of the foal may be ascertained by measuring the fore-limb from the fetlock to the elbow and multiplying it by two.

The hind-quarters of the foal are in a more advanced state of development than the fore: the shoulders are very oblique, the chest contracted and shrunken-looking, and neither shoulder nor chest contains much muscle. The oblique position of the scapula is due to the weight of the body on the limbs, the weakness of the muscles at this part allowing the angle formed by the scapula and humerus to be considerably closed, and the shoulder-joint to bulge. The head of the foal is prominent over the brain and depressed over the nasal bones. The hair is fully developed but woolly, that of the mane being scanty and of the tail curly, while the colour of the body-hair is light of its kind. A similar deficiency of pigment is observed in the iris.

TABLE SHOWING THE LENGTH OF THE BONES OF THE LIMBS OF THE FOAL AND ADULT HORSE.

	Adult Horse.	Foal of Six Weeks.	Difference.
Scapula - - -	15 in.	8¼ in.	6¾ in.
Humerus - - -	12 in.	8 in.	4 in
Radius and ulna - -	18 in.	12 in.	6 in.
Knee-joint - - -	3½ × 3½ in.	3 × 3 in.	½ in.
Metacarpal - - -	9½ in.	8¾ in.	¾ in.
Suffraginis - - -	3½ in.	3 in.	½ in.
Femur - - -	17 in.	10½ in.	6½ in.
Tibia - - - -	13½ in.	9½ in.	4 in.
Calcis - - - -	6 in.	5 in.	1 in.
Metatarsal - - -	11 in.	10 in.	1 in.
Suffraginis - - -	3½ in.	3 in.	½ in.

The rate at which the foal increases in weight, and other circumstances connected with its nutrition, were made the subject of inquiry by Boussingault.* He found that the mean weight at birth was 51 kilogrammes (112 pounds), that during the first three months the daily increase in weight was 1 kilogramme (2·2 pounds), from three up to six months the increase was 0·6 kilogramme (1·3 pounds), and from six months up to three years of age the increase was at the rate of 0·32 kilogramme (0·7 pound) per diem. The influence of feeding on development is most remarkable. Not only does the body increase in size and weight, but the animal presents the appearance of the adult, so that a thoroughbred at two years old is 'furnished' and looks as old as an ordinary horse at four years old. Calves, according to Torcy,* have a mean weight at birth of 35 kilogrammes (77 pounds), the daily increase during the first two years being 0·7 kilogramme (1·5 pounds). With sheep the daily increase in weight is more rapid. A lamb will in ten days gain 50 per cent. on its original weight, will double its weight at the end of the first month, and treble it at the end of the second. Swine present, however, the most rapid increase in weight, for, according to the authorities quoted, a pig will increase 20 per cent. in its weight per diem during the first week, and up to the end of the first year will add 0·2 kilogramme (0·44 pound) daily to its body weight.

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* Quoted by Colin.

The relative rate of growth of each part is not the same. The eyes, ears, brain, kidneys, and liver grow less rapidly than the other parts, owing to their relatively large size at birth. The greatest increase is in the skeleton and muscles, and to the rate of this increase we have just alluded; the least increase is in the eyes and the ears and the limbs below the knee and hock. Few observations have been made on the rate of growth. Percival* many years ago drew up a table, which he considered very imperfect, of the rates at which some horses of his regiment grew, from which he showed that the increase in height between two years and three years was on an average 1 inch, between three years and four years $\frac{1}{3}$ inch, and between four years and five years $\frac{1}{3}$ inch. Some of the horses did not grow.

Of 35 two-year-olds, 2 did not grow during the year.
Of 144 three-year-olds, 17 did not grow during the year.
Of 48 four-year-olds, 7 did not grow during the year.
Of 11 five-year-olds, 2 did not grow during the year.

There can be no doubt that many horses grow much more than $\frac{2}{3}$ inch between three and five years, and many grow up to their sixth year.

The writer measured the daily growth of a foal for three months, the observations being made at the withers and croup. The animal during this period grew, on an average, 1 inch every eight days. The most rapid growth occurred shortly after birth and was 1 inch in three days. At the withers and croup the rate of growth was practically equal.

During the time the calf and foal are receiving their mother's milk the urine is acid, for the reason that the animal is practically carnivorous. Once a vegetable diet is taken, the urine becomes alkaline and, it is probable, decreases in quantity. The activity of certain glands, such as the thymus, becomes considerably reduced as the animal grows, and the gland finally disappears at the adult period. One characteristic of the young animal is the necessity for sleep and rest. It is during these that the tissues make the immense strides noticeable during the first few weeks of life.

Dentition commences immediately at birth, if it has not already commenced *in utero*. The tables on p. 815 show the period at which changes take place in the teeth from birth to adult age:

The periods of eruption and change of the molar teeth are liable to considerable variation.

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* 'Lectures on Form and Action.'

HORSE.

	Eruption.	Change.
Incisors :		
Central	At birth or shortly after.	$2\frac{1}{2}$ years.
Lateral	1 to 2 months.	$3\frac{1}{2}$ years.
Corner	7 to 8 months.	$4\frac{1}{2}$ years.
Molars :		
First	At birth.	$2\frac{1}{2}$ years.
Second		3 years.
Third		About $3\frac{1}{2}$ years.
Fourth	About 1 year.	
Fifth	About $2\frac{1}{4}$ years.	
Sixth	About $3\frac{1}{2}$ to 4 years.	
Canines	About $4\frac{1}{2}$ years.	

OX.*

	Eruption.	Change.
Incisors :		
Central	At or soon after birth.	$1\frac{9}{12}$ years.
Middle		$2\frac{2}{12}$ to $2\frac{6}{12}$ years.†
Lateral		$2\frac{6}{12}$ to 3 years.†
Corner		$2\frac{10}{12}$ to $3\frac{6}{12}$ years.†
Molars :		
First	At birth.	About $2\frac{3}{12}$ years.
Second		About $2\frac{3}{12}$ years.
Third		About $2\frac{6}{12}$ years.
Fourth	6 months.	
Fifth	About 12 months.	
Sixth	21 months.	

SHEEP.

	Eruption.	Change.
Incisors :		
Central	At birth or soon after.	About 1 year.
Middle		About 2 years.
Lateral		Soon after 2 years.†
Corner		About 3 years. †
Molars :		
First	At birth or soon after.	Soon after 18 months.
Second		
Third		About 2 years.
Fourth	3 months.	
Fifth	9 months.	
Sixth	18 months.	

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* The age of the ox, sheep, and pig is tabulated from the data given by Professor Brown in his 'Dentition as Indicative of the Age of Animals'; the observations were made by Professor Simonds.

† There is considerable variation in the date of development of these teeth.

PIG.

	Eruption.	Change.
Incisors :		
Central	1 month.	12 months.
Lateral	2 months.	18 months.
Corner	At birth.	8 months.
Molars :		
First	1 month.	About 15 months.
Second		
Third		
Fourth	5 months.	
Fifth	10 to 12 months.	
Sixth	18 months.	
Premolars	5 months.	
Tusks	At birth.	9 months.

In all these tables the periods given are those of eruption only. The teeth are not fully developed for some time later, which varies from four to six months in the horse to a month in the pig and ruminant. B. Clark, nearly 100 years ago, gave a table showing the rate of growth of the temporary and permanent incisors of the horse from the time of eruption until the teeth met. It is remarkable that this question does not appear to have since attracted attention. He gave two months as the period of growth of the first and second temporary pair, and three months for the third pair. In the permanent incisors he states the period of growth of the first pair is one year, and of the second and third pairs each six months.

The completion of dentition usually marks the age of maturity. The uncastrated animal presents very distinctive features as compared with the female—viz., greater bulk, a heavy crest and neck, and a harsher voice; the castrated horse more closely resembles the mare. No such difference in the date of maturity as is observable in the human family exists between the male and female of the horse tribe. The mare arrives at maturity at the same time as the horse, and the castrated animal is not deficient in stamina, strength, or capacity for work. Moreover, castration in the horse does not lead to a deposition of fat in the body (see p. 379).

Decay.—It is doubtful to what age a horse would live if not subjected to domestication, but we may safely say that at seventeen years old, which probably represents thirteen years' work, the powers of life in the majority of them are on the wane, though at this period some may be found in full possession of life and vigour. These are probably cases of a survival of the fittest, and cannot be taken as a general guide. As a broad rule it may be stated that an old horse is liable to be killed by a hard day's work, and in this sense he is certainly old at seventeen; what he is especially deficient of at this period of life is recuperative power.

It has been pointed out (pp. 62 and 100) that the horse, unlike man, does not fail in his heart and arteries in consequence of increasing age. It is not, therefore, a matter for surprise that up to a late period of life he does not seriously lose his capacity for work. In this respect he offers a great contrast to man. At forty years of age there are few men capable of undergoing fast muscular work on their own limbs, for not only are the muscles slower in responding, but the effort required is greater. A child may indeed, execute with ease muscular movements which would produce a punishing effect on a middle-aged man. If it be accepted that a horse of fifteen is comparable to a man fifty years of age, then it is certain no man of fifty can perform the relative amount of work which a horse can at the corresponding age. It may, perhaps, yet be shown that the vertical position of man exercises a strain on the heart and vessels which is absent in the horizontally placed animal. Or there may be some actual defect in the skeletal muscles of man, the outcome of age, which is unknown in the horse. Trotting work soon wears a man out; the Japanese or Natal coolie, who pulls a light cart containing one or two people, only lasts three years. He then has to look for lighter employment. A horse performing relatively equivalent work would last much longer.

Doubtless the work performed by horses is the chief cause of their decay, for their legs always wear out before their bodies. But apart from this, changes in their teeth, such as the wearing away of the molars, appear to prevent many of them from reaching a ripe old age. Instances are on record of horses attaining the age of thirty-five, forty-five, fifty, and one animal is known to have lived to sixty-three years of age.* Blaine† appears to

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* Bracy Clark, in his 'Podophthora,' quoting from the *Liverpool Advertiser*, said there was a cart-horse on the canal near Warrington sixty-three years of age. Clark knew of a hunter fifty-two years of age that had never been out of the hands of the man who bred him. In a morning paper of May 17, 1911, it was stated that a farmer in the Lake district owned a horse forty-three years of age which still occasionally worked.

The age at death of some famous racehorses is given in the following table:

Eclipse	26 years.	Bend Or	26 years.
Parrot	36 ,,	Queen's Birthday	26 ,,
Pocahontas	33 ,,	Marcion	23 ,,
Touchstone	30 ,,	Ladas	23 ,,
Hermit	29 ,,	Cherry Tree	26 ,,
Melton	29 ,,	Collar	19 ,,
St. Simon	27 ,,	William the Third	19 ,,
King Tom	27 ,,		

† 'Outlines of the Veterinary Art.'

have gone very carefully into the question of old age in equines, and he drew the following comparison, which is doubtless very close to the truth: 'The first five years of a horse may be considered as equivalent to the first twenty years of a man. Thus, a horse of five years may be *comparatively* considered as old as a man of twenty; a horse of ten years as a man of forty; a horse of fifteen as a man of fifty; a horse of twenty as a man of sixty; of twenty-five as a man of seventy; of thirty as a man of eighty; and of thirty-five as a man of ninety.'

The indications of advanced age in horses are well marked, apart from those connected with the length, shape, and colour of the teeth: the edge of the lower jaw becomes sharp, the supra-orbital fossa deep, the eyelids wrinkled; white hairs may appear on the face and elsewhere, while black horses may turn white, though this is unusual. A hollow back is very greatly intensified with age; the joints of the limbs show the effects of work, and the gait has lost its elasticity.

In the case of animals intended for food the question of decay does not arise. In the carnivora Mr. H. Gray informs the writer that in the dog at about eight years old, tumours, carcinoma, cardiac murmurs, chronic orchitis, sarcoma of the testicle, enlargement of the prostate, catarrhal endometritis, chronic mammitis, and cirrhosis of the liver with ascites are liable to appear. In the cat he states that mammary cancer, especially of the pectoral glands, is common at about fourteen to sixteen years of age. The frequency of malignant tumours is remarkable; they are not evident in the horse, if we except grey animals, where melanotic growths are a frequent accompaniment of old age.

The **duration of life** in the various domesticated animals is given by Crisp* as follows:

Horse - -	25 to 35 years.	Sheep - -	15 years.
Ass - -	30 to 40 years.	Pig - -	12 to 16 years.
Ox - -	15 to 20 years.	Dog - -	14 years.
Goat - -	15 years.		

It is believed these observations were made under the favourable conditions of animals in captivity (Zoological Gardens), well fed and looked after, and the figures are in consequence high.

Selecting thoroughbred stock as the type of horse placed under the most favourable conditions, we find the mean age at death of both stallions and mares to be a little under twenty years.

Mr. H. Gray informs the writer that the larger the breed of dog the shorter its life. Great Danes are old at eight to nine years, spaniels, collies, etc., at ten to twelve years, terriers at twelve to fourteen years. The smaller breeds live sometimes to sixteen and eighteen years; dachshunds may live to eighteen or nineteen years, and Maltese to twenty to twenty-two years. In the dog, as with man, a long life is hereditary. The life of the cat is longer than that of the dog.

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* *Op. cit.*, p. 757.

We have already seen that in the herbivora and carnivora there is no 'change in life' as effecting either male or female, and that both are virile in old age.

Death.—Death from senile decay in the horse is a matter of rare occurrence. It is seldom that an animal is taken such care of that the tissues are worn out by age, or that he is allowed to live until the breath of life passes gradually from the body.

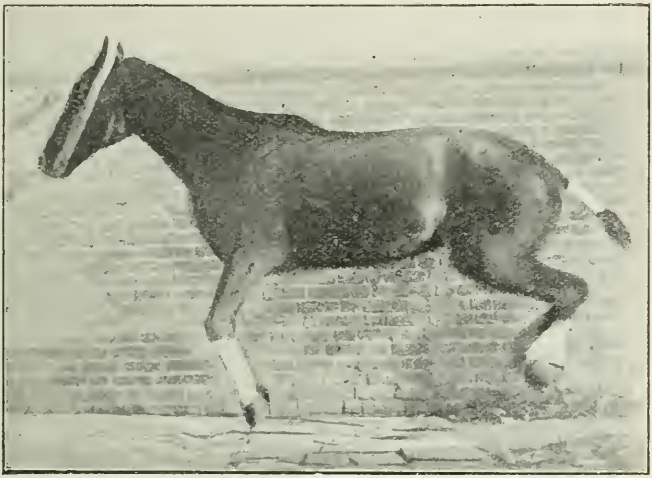

Fig. 271.—Convulsive Limb Movements at the Moment of Brain Destruction.

Note the tail is affected as well as the limbs. The bandages were put on to assist the plate.

Sentiment plays no part in horse management. A useless mouth is one to be got rid of. In consequence, the majority of horses meet either with a violent death or one the result of disease. Under good hygienic conditions the general annual death-rate may be taken at 1·5 per cent. To this, however, must be added a fluctuating loss due to destructions for injury, which may be stated at about 1 per cent., depending on the occupation.

Natural death is described as commencing either at the heart, lungs, brain, or blood. Probably the few cases of natural death which occur may be attributed to failure of the heart's action; but from what is known of the physiology of the heart, respiration, and blood, it is very difficult to separate these in discussing the causes of death, as one is so largely dependent on another. The cessation of the heart's action may be looked upon as the termination of life.

We cannot enter upon the cause of death resulting from disease, except to notice the interesting fact that horses seldom die quietly. A large majority of them die in powerful convulsions, fighting or struggling to the last, lying on the side, and galloping themselves to death. This is especially marked in acute abdominal trouble, or other painful conditions. The struggles at the end should not be mistaken for pain: the animal is quite unconscious. The violent convulsions which occur at the last moment are not present in death from acute chest diseases; such cases stand persistently to the last, and either drop dead or die very shortly after falling.

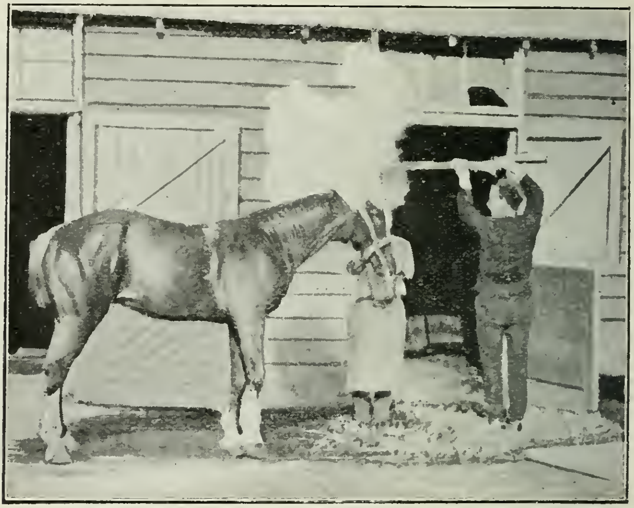

FIG. 272.—BRAIN DESTROYED BY A CHARGE OF SHOT.

The head has slightly dropped; the muscles of the quarters are preparing to contract, as may be seen by their outline; the tail is also turned to one side, and the heel of one fore-limb has left the ground. There is nothing, however, to indicate the fact that the horse is dead.

In violent death by destruction of the brain in horses, remarkable muscular contractions of the limbs occur. These cannot be seen with the unaided eye, as they are so rapid, but are readily revealed by the camera (Fig. 271). In spite of their rapidity, a distinct interval occurs between brain destruction and muscular contractions. In Fig. 272 the brain was destroyed by a charge of large shot, yet the horse is still standing, the impulses producing convulsive limb movements not yet having had time to pass out. At the moment of violent death the bladder and rectum are emptied, the penis protruded, the horse sweats on the inside of the thighs, the pupils dilate widely, and occasionally, when all seems at an end, the *panniculus* is called into play, and the animal may shake the skin with remarkable vigour, as if to dislodge a fly. The heart may continue to beat for a minute or two, but the respirations cease. As life is being extinguished the *ligamentum nuchæ* exercises its elastic recoil in the absence of muscular resistance, and the head is drawn back momentarily with slight jerks until the muzzle projects.*

Soon after death *rigor mortis* appears (see p. 451), and within a short time tympany of the abdomen is apparent in the herbivora, reaching such a degree in a few hours, especially during warm weather, that post-mortem ruptures of the diaphragm and other viscera are exceedingly common. The explanation of the tympany is the considerable amount of gas generated by the fermentative decomposition of vegetable food. In death-stiffening the flexor muscles of both fore and hind limbs contract in excess of the extensors, so that the heels of the feet are slightly drawn up; the ears are also drawn back, and in the course of an hour or two the pupils are closely contracted.

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* At p. 654 reference has been made to the elastic nature of the ligamentum nuchæ. By an oversight its functions were not referred to in dealing with the subject of posture, p. 435. The chief function of this elastic ligament is to assist the muscles in keeping the head extended, as, for example, during the prolonged act of grazing. It also assists in supporting the head, but this is a subordinate function as the funicular portion may be completely divided without causing the head to droop.

CHAPTER XX

THE CHEMICAL BASIS OF THE BODY*

By Professor T. H. Milroy, M.D.

Our knowledge of the chemical composition of the animal organism is almost entirely based upon the analysis of the various tissues and fluids, not as they exist during life, but after their removal from the living structure. A great variety of elements is met with, usually in combination, although in a few cases—for example, the oxygen (partly) and the nitrogen dissolved in the blood—they are met with in the free state. The most important elements are carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus, chlorine, iodine, traces of fluorine, sodium, potassium, calcium, magnesium, and iron. These elements are met with either in organic or in inorganic compounds.

The chemical constituents of the body may be considered under the following headings: I. Gases; II. Water; III. Inorganic Salts; IV. Organic Compounds.

I. The **Gases** found are oxygen, nitrogen, hydrogen, carbon dioxide, sulphuretted hydrogen, and marsh gas. **Oxygen** is the most widely distributed of the elements, forming one-quarter by weight of the atmosphere, and eight-ninths by weight of water. By means of its compounds it forms one-half by weight of the earth's crust. It is practically the only element which enters the animal or vegetable body in a free state, and in plants it does so only to a limited extent, for these obtain the bulk of their oxygen through the decomposition of carbon dioxide and water. In the animal body it exists free and combined in some of the body fluids, such as blood; others, such as lymph, contain only traces, and none can be obtained from the most bulky tissue of the body—*i.e.*, muscle. Of the two great cavities of the body—the chest and abdomen—one is remarkable for containing the oxygen absorbing and distributing apparatus, the other contains the digestive canal, which carries out its work in the entire absence of oxygen. **Nitrogen** exists largely in a free state, since it forms no less than four-fifths of the atmosphere, while it has but little affinity for other elements. In the form of ammonia, nitrous and nitric acids, it enters the plant through its roots; as protein it enters the animal, leaving it as urea, etc., which by decomposition readily yields ammonia. The animal cannot utilise free nitrogen any more than the plant can, though leguminous plants utilise atmospheric nitrogen by symbiotic co-operation with nitrifying bacteria. There are nitrifying and denitrifying bacteria. The former oxidise ammonia and nitrites into nitrates, and are capable of assimilating the free nitrogen of the atmosphere, which they fix and supply to the plant. The latter set nitrogen free by reducing nitrates to nitrites, and decomposing nitrites into nitrogen. From the nitrifying bacteria in plants protein can be built up out of inorganic salts in the absence of chlorophyll. **Carbon** is present in the atmosphere in small amounts united to oxygen—*i.e.*, in the form of carbon dioxide. It is only in this form that it can be taken up by plants, which in their special laboratory split off the oxygen molecule and store up the carbon, returning the oxygen to the air, and thus supply to the atmosphere that element of which animals are continually depriving it. Under the influence of the ultraviolet rays in light, the green leaves of plants are capable of manufacturing sugars and starches from carbon dioxide and water. Carbon enters the animal system with the carbon of the food, and leaves it either as carbon dioxide or in compounds, such as urea; as carbon dioxide it is again taken up by the plant. There is no solid or fluid tissue of the body free from carbon dioxide. It is the most widely distributed gas in the body.

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* It is not intended in this chapter to do more than to elucidate and supplement some of the chemical statements scattered throughout the previous chapters.

II. **Water** forms 60 per cent. of the whole body, the bulk of which is taken in with the food, only a small quantity being produced in the organism. The water supplied to the system furnishes no potential energy, but it is essential in order that the sources of the potential energy may be enabled to transform their potential energy into the kinetic form. The amount of water met with in various tissues ranges from the mere trace existing in such structures as the enamel and dentine of the fully developed tooth to the very high percentage met with in such fluids as the sweat and saliva (over 99 per cent. in certain cases). As the physiological significance of many dissolved constituents depends upon the degree of their dissociation, which increases with dilution and diminishes with increasing concentration, any interference with the normal intake gives rise to the most serious disturbances (see p. 392).

III. **Inorganic Salts.**—The most important members of this class are the chlorides, phosphates, carbonates, and sulphates of sodium, potassium, calcium, and magnesium (see p. 382 *et seq.*).

1. The chlorides are the most widely distributed salts in the body, appearing as valuable constituents practically in all the tissues and fluids. They contribute largely to the total saline concentration in the various fluids, and thus must play an important part in the regulation of fluid exchange within the tissues. Certain proteins—for example, globulins—require these salts for their solution. As the sole source is from preformed salt in the food, and as the urine and sweat carry away daily a fairly large amount, their replacement necessitates an adequate supply in the dietary. As the source of the hydrochloric acid of the gastric juice, the chloride is necessary for certain ferment actions. The chloride present in largest quantity in the body is the sodium salt, and it is in the tissue fluids rather than in the intracellular substance that the concentration is highest.

2. The phosphates may be derived from various sources. In the first place, they may be taken as inorganic salts in such foods as oats, mainly as the magnesium salts. By collecting in the bowels, these salts produce the ammonio-magnesium phosphate calculi so common in horses. The foods richest in phosphoric acid are oil cake and

bran, while hay and straw are poorest in this substance. Phosphoric acid is principally excreted by herbivora with the fæces, only small quantities passing away with the urine.

A portion of the phosphates excreted is derived from organically bound phosphorus in foods or tissue elements, as, for example, the lecithins, nucleo-proteins, and phospho-proteins.

The phosphates of the alkalies form important constituents of the body fluids and also of the cell protoplasm, while those of calcium and magnesium contribute largely to the ash of bone.

3. The carbonates, and especially the bicarbonates, of the alkalies are extremely important constituents of the body fluids. The bicarbonates play an important rôle in determining the reaction of the body fluids, as has been described under the Reaction of the Blood. They constitute the end products of the oxidation of the salts of such organic acids as citric, malic, and tartaric acids. They are met with in the form of calcium carbonate in the urine of herbivora, being kept more or less completely in solution by carbonic acid. Calcium carbonate also occurs along with the phosphate in the ash of bones.

4. Sulphates occur in small quantity in the body fluids, being partly derived from the sulphur present in organic combination in the food proteins (exogenous), and partly from the disintegration of the tissue proteins (endogenous).

The forms in which the sulphur occurs in the urine and in the bile are referred to in the sections dealing with those fluids.

The important functions of the various salts are discussed under metabolism (p. 382 *et seq.*), but these may here be shortly summarised. Upon the saline concentration of the body fluids the osmotic pressure most largely depends, and thus a certain "isotonic" value of these fluids is necessary in order to maintain the integrity of the cell elements in contact with the fluids. Thus any solution which shows a different molecular concentration from the normal blood-plasma would disturb the osmotic equilibrium of the medium were it introduced into the circulation. Hamburger has largely made use of the red cells for determining the isotonic values of various saline solutions. If the salt solution be above the normal value (hypertonic), shrinkage of the red cells, or crenation, occurs; while if it be below the normal (hypotonic), distension and finally rupture of the red cells occur, with resultant hæmolysis. The alkaline carbonates play an important part at least as storehouses of the important end product of metabolism, carbonic acid. Very slight disturbances in the amounts of other salts may give rise to very distinct alterations in the excitability of tissues. Thus, removal of the small quantity of calcium from the fluids used for heart perfusion will give rise to cessation of the beat, while a slight excess will produce an increased tonus of the cardiac muscle. Potassium salts act as the antagonists of the calcium ones.

IV. **Organic Compounds** are most conveniently subdivided into (1) **nitrogenous,** and (2) **non-nitrogenous,** under the former being included the proteins and their cleavage products, and under the latter the fats and carbohydrates. The proteins constitute the most important constituents of the body. As food-stuffs and constituents of the tissues they are irreplaceable, and the large nitrogen output from the body daily shows how active a part they play in bodily metabolism. All are characterised by certain very distinctive physical and chemical properties. They belong to the important group of colloids referred to as emulsoid colloids. An emulsoid colloidal system shows a high viscosity and a great tendency to foam formation. It does not show any difference in electrical charge between the internal and the external phase. High electrolyte concentration is necessary to bring about a coagulation, which is in most cases reversible. In each of the above respects the emulsoid differs from the suspensoid system.

The emulsoid system is closely allied to a true solution, and hence protein solutions may be studied in the same way as true solutions.* Such solutions show an infinitely slow rate of diffusion through dialysing membranes, owing to the large size of the protein molecule. In virtue of their colloidal character they constitute the important viscous element of the blood, and by means of their indiffusibility they regulate and control fluid exchange, thus often counteracting filtration, which would otherwise occur under a hydrostatic pressure. Chemically they give a number of reactions which can only be satisfactorily dealt with in practical textbooks. These mainly depend upon the existence in the protein molecule of certain groups with characteristic reactions. The protein molecule is a very large one, as is shown by the extremely small osmotic pressure exerted by fairly strong solutions. Determinations of the molecular weight are extremely difficult, and have given rise to very divergent results, partly due to variations in the size of molecular aggregates and partly to admixture with salts. Hüfner and Gausser's determinations of crystallised hæmoglobin most carefully prepared gave molecular weights of 15,000 to 18,000, while Sörensen's determinations of crystallised egg-albumin gave the molecular weight of the anhydrous protein as 34,000.

The percentage composition of proteins varies, as is shown in the following table:

	Per Cent.
Carbon - - - -	51·5 to 54·5
Hydrogen - - - -	6·9 ,, 7·3
Oxygen - - - -	20·9 ,, 23·5
Nitrogen - - - -	15·2 ,, 17·0
Sulphur - - - -	0·3 ,, 2·0

The proteins may be classified as follows:

1. Protamines.
2. Histones.
3. Albumins and globulins.
4. Glutelins and gliadins (vegetable proteins).
5. Conjugated proteins (nucleo-proteins, gluco-proteins, chromoproteins).
6. Phospho-proteins.
7. Sclero-proteins.
8. Derived proteins (meta-proteins, proteoses, peptones, polypeptides).

The protamines are of strongly basic character, and are found in combination with nucleic acid in the form of nucleo-proteins. They may be obtained from ripe fish spermatozoa, arginine, a diamino-acid, forming a characteristic constituent.

The histones are also strongly basic. They have a high nitrogen percentage (up to 20 per cent.), and evidently are intermediate between protamines and the albumin class. Their yield of arginine is smaller.

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* Sörensen's 'Studies on Proteins,' *Comptes Rendus des Travaux du Laboratoire de Carlsberg*, vol. xii., 1917.

The albumins and globulins are heat-coagulable proteins, which contain sulphur, but little or no phosphorus. The albumins are soluble in water, while the globulins are only soluble in dilute salt solutions. The most important examples of this class are the serum-albumin and serum-globulin of the blood, but there are also many vegetable globulins, such as edestin, a crystallisable protein obtainable from hemp-seed.

The glutelins and gliadins are vegetable proteins present in many kinds of seeds. The former are insoluble in alcohol and neutral aqueous solutions, the latter (present in the seeds of cereals—*e.g.*, gliadin of wheat and rye, hordein of barley, zein of maize) are soluble in alcohol, but not in water. The products of their hydrolysis are different; thus gliadin and hordein yield more glutamic acid and less arginine than the glutelins. Zein yields more leucine and less glutamic acid than gliadin and hordein.

The conjugated proteins are interesting bodies which possess in addition to the simple protein another substance, known as the prosthetic group. The nucleo-proteins vary in complexity, the simplest being those which occur in fish spermatozoa already referred to. They are also present in large quantity in such organs as the thymus and pancreas. Under the action of ferments such as trypsin they break down into nucleic acid and the usual products of proteolysis.

The nucleic acid can be broken down by acids into a number of products—carbohydrates, phosphoric acid, pyrimidine, and purine bases. The structure of the nucleic acids is a complex one, the simplest forms consisting of one molecule each of acid, base, and sugar, a combination found in guanylic and inosinic acids (Levene and Jacobs).

Chromo-proteins: The most important representative of this group is hæmoglobin, the properties of which have been already described.

The most important gluco-proteins belong to the class of mucins and mucoids. An important derivative of these bodies is an amino-glucose, glucosamine.

The phospho-proteins, like the nucleo-proteins, contain phosphorus, but differ from the latter in yielding on hydrolysis no purine nor pyrimidine bases. Caseinogen of milk and vitellin of egg-yolk are the most important representatives.

Sclero-proteins, found in skeletal and connective tissues, are represented by gelatin derived from skin and cartilage, elastin from elastic fibrous tissue, keratin from horn, hair, and nails, and many others.

Derived proteins are obtained by the partial hydrolysis of proteins. Examples of these are the meta-proteins (acid and alkali), and later products of hydrolysis such as proteoses, peptones, and polypeptides. The polypeptides are the most interesting representatives of this class, because their structure is better understood than that of the others. They are made up of amino-acids which are joined up with one another in amide form, the carboxyl group of one amino-acid being linked to the amino-group of another. Two three, four, or more amino-acids may be so joined together, constituting the bodies known as di-, tri-, tetra-, and poly-peptides. A simple example of a di-peptide is glycyl-glycine, two molecules of glycine (amino-acetic acid) being linked together—

$$H_2N.CH_2.CO.NH.CH_2.COOH.$$

Products of the Hydrolysis of Proteins.—When proteins are subjected to the action of acids, alkalies, or ferments under suitable temperature conditions, they undergo hydrolytic decomposition, and furnish a great variety of cleavage products, many of which are met with in the animal organism.

These products may be classified as follows:

Monobasic mono-amino-acids :

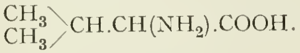
Glycine (amino-acetic acid)—

$$(NH_2).CH_2.COOH.$$

Alanine (α-amino-propionic acid)—

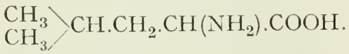
$$CH_3.CH.(NH_2).COOH.$$

Valine (α-amino-isovaleric acid)—



$$\begin{matrix}CH_3\\CH_3\end{matrix}\!>\!CH.CH(NH_2).COOH.$$

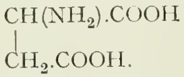
Leucine (α-amino-isobutyl-acetic acid)—



$$\begin{matrix}CH_3\\CH_3\end{matrix}\!>\!CH.CH_2.CH(NH_2).COOH.$$

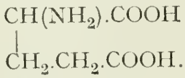
Dibasic mono-amino-acids :

Aspartic acid (α-amino-succinic acid)—



$$\begin{array}{l}CH(NH_2).COOH\\ |\\ CH_2.COOH.\end{array}$$

Glutamic acid (α-amino-glutaric acid)—



$$\begin{array}{l}CH(NH_2).COOH\\ |\\ CH_2.CH_2.COOH.\end{array}$$

Hydroxy- and thio-amino-acids :

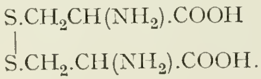
Serine (α-amino-β-hydroxy-propionic acid)—

$$CH_2.OH.CH.NH_2.COOH.$$

Cysteine (α-amino-β-thiolactic acid)—

$$CH_2.SH.CH(NH_2).COOH.$$

Cystine (dithio-amino-propionic acid)—



$$\begin{array}{l}S.CH_2CH(NH_2).COOH\\ |\\ S.CH_2.CH(NH_2).COOH.\end{array}$$

Diamino-acids :

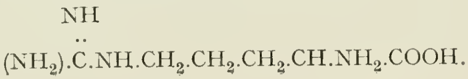
Ornithine ($\alpha\delta$-diamino-valeric acid)—

$$(NH_2).CH_2.CH_2.CH_2.CH(NH_2).COOH.$$

Lysine ($\alpha\epsilon$-diamino-caproic acid)—

$$(NH_2).CH_2.(CH_2)^3.CH.NH_2.COOH.$$

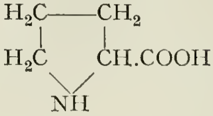
Arginine (α-amino-δ-guanido-valeric acid)—



$$(NH_2).\overset{\overset{NH}{\cdot\cdot}}{C}.NH.CH_2.CH_2.CH_2.CH.NH_2.COOH.$$

Heterocyclic amino-acids :

Proline (α-pyrrolidine-carboxylic acid)—



Histidine (α-amino-β-iminazole-propionic acid).
Tryptophane (indole-α-amino-propionic acid).

Aromatic amino-acids :

Phenylalanine (α-amino-β-phenyl-propionic acid).
Tyrosine (α-amino-ρ-hydroxy-phenyl-propionic acid).

From the action of anaerobic or putrefactive bacteria the amino-acids are broken down into various amines, generally with a loss of carbonic acid. Thus leucine furnishes isoamylamine, ornithine tetramethylene diamine, lysine pentamethylene diamine, tryptophane indole ethylamine and histidine, iminazole ethylamine. Aerobic bacteria oxidise the amino-acids to fatty acids with one atom less with the loss of NH_3 and CO_2.

It is important to know the nature and amount of the amino-acids obtainable by hydrolysis from various proteins.

	Hæmoglobin.	Caseinogen (Cow).	Keratin.	Gliadin.	Edestin.	Salmine.
Glycine	—	—	0·3	0·02	3·8	—
Alanine	4·19	0·9	1·2	2·0	3·6	—
Valine	—	1·0	5·7	0·2	+	4·3
Leucine and isoleucine	30·0	10·5	18·3	5·61	20·9	—
Aspartic acid	4·43	1·2	2·5	0·58	4·25	—
Glutamic acid	1·73	11·0	3·0	37·53	6·3	—
Serine	0·56	0·23	0·7	0·13	0·33	7·8
Cystine	0·31	+	7·0	0·45	0·23	—
Lysine	4·28	6·0	+	—	1·0	—
Arginine	5·42	4·8	2·3	3·16	11·7	87·4
Proline	2·34	3·1	3·6	7·06	4·1	11·0
Histidine	10·76	2·6	—	0·61	1·1	—
Tryptophane	+	1·5	—	+	+	—
Tyrosine	1·33	4·5	4·6	1·2	2·11	—

The various proteins met with in the animal organism are thus best characterised by the amounts of the various amino-acid derivatives obtainable from them. These constitute the building-stones of the proteins, and metabolism is largely concerned in the separation and selection of these acids, some for complete disintegration and others for synthesis. Although, as already stated, the tests for proteins can only be satisfactorily dealt with in practical textbooks, it is advisable to refer briefly to the most characteristic reactions.

Tests for Proteins.—There are certain chemical tests which apply to the entire group of protein bodies, and others which are distinctive of members of the group. Their reactions are based on colour tests, precipitation, or coagulation.

Colour Tests—Xantho-Proteic Reaction.—Solutions of protein heated with strong nitric acid turn yellow, and on the addition of ammonia or caustic soda change to orange. This reaction is considered to be due to the presence in the molecule of some group of the aromatic series.

Millon's Reaction.—Millon's reagent is a mixture of mercurous and mercuric nitrates in the presence of nitric acid. When boiled with a protein solution, the mixture turns red, and the same colour is imparted to a precipitate should it occur. This reaction is supposed to be due to the presence of tyrosine in the molecular grouping, and is therefore not given when this is absent.

Piotrowski's Reaction.—To the solution of protein an excess of strong solution of caustic soda is added, and one or two drops of a 1 per cent. solution of copper sulphate. A violet colour results in the presence of native protein, and a rose-red colour in the presence of proteoses and peptone. The essential feature is that the colour must be a purple, either red or blue. When protein in any form is absent, the solution remains blue. The term *biuret* is applied to this test, as a similar reaction is given with biuret, which is formed by heating urea.

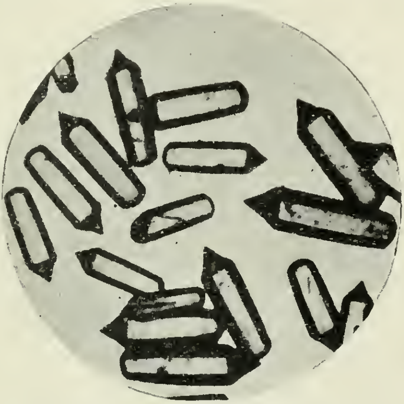


FIG. 273.—ALBUMIN CRYSTALS FROM HORSE-SERUM (GÜRBER).

Adamkiewicz's Reaction.—A mixture of one volume of concentrated sulphuric acid and two volumes of glacial acetic acid, when added to a solution of protein, produces a reddish-violet colour and slight fluorescence. The reaction is due to the presence of tryptophane in the molecule.

The *precipitation* of proteins is brought about on the addition of mineral acids, such as nitric; salts of the heavy metals—for instance, acetate of lead or mercuric chloride—and by boiling; also by excess of alcohol; neutral salts of the alkalies—*i.e.*, sodium chloride and ammonium sulphate—to the point of saturation, and in many other ways. Halliburton draws attention to the necessity for distinguishing between coagulation and precipitation. For instance, a protein, on heating or on adding nitric acid, is coagulated; the precipitate is insoluble, but precipitates obtained by the addition of such substances as ammonium sulphate are soluble, and can readily be sent back into solution. To these the term 'precipitate' especially applies. The circumstances under which such precipitates are obtained have been mentioned under the head of Albumins and Globulins.

As already stated, several proteins may be obtained in crystalline form—for example, egg-albumin, the serum-albumin of the horse (Fig. 273), hæmoglobin, and many plant proteins. In all careful analyses of the proteins it is necessary to obtain the material in as pure a form as possible, hence the great advantage of crystallised proteins.

The Non-Nitrogenous Constituents.

1. The fats and oils are glycerol esters (glycerides) of the fatty acids. The fatty acids may differ in number and in character; thus there may be di- or tri-glycerides with the same or different fatty acid radicles. They may be extracted from the tissues by means of ether and other solvents of a like nature. They constitute the most important ether-soluble constituents of the tissues, but there are also included in such extracts other bodies of a somewhat fatty nature which differ from the fats and oils in containing nitrogen, phosphorus, or a carbohydrate group. The term *lipoid* has been used, not always with the same significance, to include bodies of this nature. There are also found in the animal and vegetable kingdom esters of higher alcohols—the waxes—such as spermaceti and beeswax.

Cholesterol, a secondary alcohol of still uncertain constitution, is very widely distributed, and forms an important constituent of certain gall-stones. It is evidently a cyclic compound with a double bond. It can replace glycerol and form esters with certain fatty acids. Iso-cholesterol is present along with cholesterol in the wool-fat of sheep, and also in sebum.

The various substances which may be found in an ethereal or alcoholic extract of the tissues may be classified as follows:

1. Neutral fats (including waxes), oils, fatty acids.
2. Cholesterol and allied bodies and their compounds.
3. Phosphatides, such as lecithin, containing fatty acids, nitrogen, and phosphorus.
4. Cerebrosides, containing fatty acids, nitrogen, no phosphorus, but a carbohydrate group.

It is evident, therefore, that the fats are closely associated with bodies containing nitrogen, and hence the classification into nitrogenous and non-nitrogenous, including under the latter fatty-like bodies, is not a correct one.

1. **Fats.**—The fats found in body-fat, milk, and the marrow of bones, are compounds formed by the union of fatty acids with glycerol. These fats are *palmitin*, *stearin*, and *olein*.

Fatty acids are formed by the oxidation of alcohols, the group being a large one. Some of the earlier members of the series, such as acetic, propionic, valeric, caproic, have been referred to in speaking of the amino-acids, for these form glycine, alanine, valine, and leucine, in the manner already described. The acids responsible for the body fats—palmitic and stearic acids—are the sixteenth and eighteenth in the *acetic* series, while oleic is the eighteenth in the *acrylic* series. A certain proportion of the fats in milk, and hence in butter, is formed from acids lower down in the acetic series, such as *caproic*, *caprylic*, and *capric acids*.

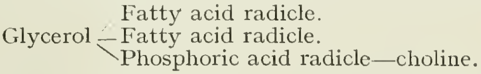
Fat is insoluble in water, and only slightly so in alcohol, but freely soluble in ether, chloroform, and benzene. When pure, it is neutral in reaction, tasteless and colourless, and by the action of caustic alkalies or superheated steam may be decomposed into its respective fatty acid and glycerol. When this splitting is brought about by an alkali, the base, sodium or potassium, at once unites with the free fatty acid and forms a salt (soap). This decomposition and saponification takes place to a greater or less extent in the intestine under the influence of the pancreatic juice and bile.

The solid fat of the body is composed principally of stearin, such as is found in the ox and sheep. The more liquid fat, such as is found in the horse and carnivora, contains palmitin, but in all cases a mixture of the three fats is obtained. Fat as it exists in the cells of the living body is, of course, in a liquid condition. Since the melting-point of palmitin is 45° C., and that of stearin 55° to 60° C., it is evident that the fluidity of living fat is due to the olein it contains, the melting-point of which is – 5° C. The amount of fat in the body must depend upon the feeding of the animal, and will obviously vary within extreme limits. In individual tissues marrow has the largest amount; nerve, brain, milk, muscle, liver, bone, bile, and blood, have proportions which decrease in the order given. The change which the fats undergo in the alimentary canal has been discussed in the chapter on the pancreas (p. 264), while the origin of fat in the body, and its function is dealt with under nutrition (p. 375).

2. **Cholesterol** ($C_{27}H_{45}OH$) is found in bile and the tissues generally, especially in nervous tissue and bone-marrow, and also very commonly in pus and various pathological effusions. It is present in small quantity in blood-serum in combination with fatty acids as esters, and also in lanolin or sheep-wool 'fat.' It crystallises from hot alcohol in thin rhombic plates with notched angles. It is readily soluble in hot alcohol, and also in acetone, chloroform, ether, and benzene. In chloroform solution it is lævo-rotatory. The chloroform solution gives certain characteristic reactions, one of the most commonly employed being Salkowski's test. On adding an equal quantity of strong sulphuric acid to the chloroform solution, the upper ($CHCl_3$) layer reddens and the lower (H_2SO_4) one appears yellow with a green fluorescence.

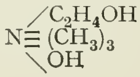
3. **Phosphatides** occur in various forms with different ratios of N : P, from 1 : 0·5 to 1 : 2.

Lecithin is the most common phosphatide. It is classified by Maclean as a mono-amino-phosphatide (N : P = 1 : 1). It is met with in practically all tissues along with fat, and its occurrence has been already frequently referred to. Its constitution may be represented as:



Fatty acid radicle.
Glycerol — Fatty acid radicle.
Phosphoric acid radicle—choline.

Choline is closely related to muscarine obtainable from certain fungi. Its constitution is:



$$N\equiv\begin{array}{l}\diagup C_2H_4OH\\ (CH_3)_3\\ \diagdown OH\end{array}$$

or trimethyl-β-hydroxy-ethyl-ammonium hydroxide. Lecithin dissolves very readily in alcohol, and differs in this respect from kephalin, which belongs to the same group of phosphatides. Kephalin does not contain choline, but another base, oxy-ethylamine.

4. **Cerebrosides,** as their name signifies, are present in brain tissue but are also met with in other parts. On hydrolysis they yield galactose.

Phrenosin and kerasin are two members of this class.*

Carbohydrates.—This important class is of the greatest interest to the physiologist, inasmuch as the bulk of material consumed as food, especially in the herbivora, consists of carbohydrate matter. It is an extensive group of bodies consisting of such substances as starch and its derivatives, the various forms of sugar, and cellulose. Though so much carbohydrate material enters the body, but little can be found in the tissues. An animal starch (glycogen) is found in the liver and other organs, minute amounts of sugar are found in the blood, and a sugar exists in milk; but very much less carbohydrate is recoverable from the body than enters it as food, for the reason that the bulk of it becomes converted into fat, or is rapidly oxidised to carbonic acid and water as a source of heat and energy to the body.

The carbohydrates may be divided into the—

Starch group, or *polysaccharoses*.
Cane-sugar group, or *disaccharoses*.
Dextrose group, or *monosaccharoses*.

Polysaccharoses—*Starch.*—The formula for starch is unknown; it is considered to be $(C_6H_{10}O_5)n$, where n is not less than 5 or 6, and is probably very much larger. The molecular weight is thus unknown.

Starch exists in plants in the form of grains, the shape of which depends upon the group from which they are derived; thus potato, bean, wheat, and other starch grains, have each a distinctive shape. The grain is composed of two parts, an envelope known as *cellulose* (amylopectin) and an interior called *granulose* (amylose). The granulose is the true starch; the cellulose is not, however, identical with the ordinary cellulose of plants. Starch is insoluble in cold water, but when boiled the grains burst, and a viscid, opaque, pasty mass results, which is not, however, a true solution of starch. A solution of starch can be obtained from this mass by *careful and limited* digestion with an enzyme, such, for instance, as human saliva, or by the action of dilute acid; when this takes place the material becomes watery, perfectly transparent, and filters readily, while previously this was impossible. To this limpid fluid the name ‘ soluble starch ’ has been given. The characteristic test for starch is the blue colour produced on the addition of iodine. Starch has no reducing action on Fehling's solution.

Dextrin.—When starch paste is acted upon by dilute mineral acid, or the enzymes found in the saliva and pancreatic juice, soluble starch is first formed as above described; but if the process be allowed to continue, further changes rapidly occur, leading to the production of dextrin and finally of sugar. There are probably several dextrins, though two are generally more particularly described —viz., *erythro-dextrin* and *achroo-dextrin*. These are distinguished from starch and from each other by their colour reactions with iodine, erythro-dextrin giving a reddish colour, while achroodextrin gives no colour. Much the same change which can thus be brought about by acting upon starch out of the body takes place more rapidly within the body. The sugar formed from the action of amylase on amylose is maltose, while hydrolysis of starch by acids furnishes glucose. The conversion of starch into dextrin and finally into sugar under the influence of certain enzymes performs a most important physiological function; neither starch nor dextrin is capable of being absorbed as such, whereas the sugar which results from this conversion is readily assimilable.

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* ‘Lecithin and Allied Substances,’ by H. Maclean. Longmans, Green and Co., 1918.

Glycogen closely resembles starch. It is found in several of the tissues of the body, and its origin and use have been previously discussed (see p. 252). It may be obtained as an amorphous white powder, readily soluble in water, and gives with iodine a port-wine colour instead of blue. By the action of acids or enzymes it is readily converted into dextrin, and finally into sugar. The sugar resulting from the action of acid is dextrose, whereas that produced by the enzyme is maltose; in the liver the sugar produced is dextrose and not maltose, and the method by which this conversion is obtained has been previously dealt with.

Cellulose, though not found in the animal body, is of great interest to the physiologist from its intimate relation to the feeding of the herbivora. The food substance in plants is locked up in a cellulose envelope, and until this envelope is broken down the material within cannot be acted upon by the digestive juices. This breaking down is accomplished by laceration during the process of mastication, but also by a subsequent digestion of the covering, by which means it is removed and the food substance exposed. The digestion of cellulose is a physiological puzzle, for the reason that no vertebrate is known to secrete a cellulose-dissolving enzyme. In certain invertebrates a true cellulose enzyme (*cytase*) is met with, and is known to be secreted in the intestinal canal. Inasmuch as the herbivora are capable of dealing with cellulose, the question of its solution is of the greatest interest. Bunge has shown that sheep can digest from 30 to 40 per cent. of the cellulose of sawdust and paper when mixed with hay. There is every reason to think that all the herbivora deal quite as thoroughly with the cellulose naturally found in their food. The question has been before us in dealing with digestion (p. 199), in which it was shown that in the case of oats the grain provided its own cellulose-dissolving ferment. It is hardly likely that the sawdust or paper in Bunge's experiment provided their own enzyme, so that it is probable the hay furnished it. Cellulose however, may be digested by the action of putrefactive organisms, either outside or inside the body. In both cases it is attended by the formation of acetic and butyric acids, and the evolution of marsh gas, carbon dioxide, and other substances. We have previously studied the facilities which exist within the body for the necessarily slow maceration of cellulose, which is the essential prelude to its solution (see pp. 224, 227 and 373).

Disaccharoses ($C_{12}H_{22}O_{11}$).—**Sucrose**, or cane-sugar, is not found as part of the animal body, but exists largely in plants, and forms a well-known supply of carbohydrate to the system. Cane-sugar does not give some of the characteristic sugar reactions; among others, it has no reducing action upon salts of copper, but by boiling with dilute mineral acids it is converted into equal parts of dextrose and lævulose, and the same change may be effected by enzymes in the stomach and small intestines. This conversion of cane-sugar is recognised by the changed action of the solution on polarised light, the rotation of the plane of polarisation being now to the left instead of to the right, as it was previously to the conversion; that is to say, it is *inverted*, hence the name *invert sugar*. If cane-sugar be injected into the circulation, it passes out of the system unaltered. Before this sugar can be assimilated, it must be converted into dextrose (see pp. 218 and 296).

Maltose is formed by the action of malt extract (diastase) on starch paste, also by the action of saliva and pancreatic juice upon starch paste and glycogen. In its reactions it corresponds closely to dextrose, but it has a one-third less reducing action upon Fehling's solution, and, unlike it, does not reduce Barfoed's reagent.* Its specific activity in rotating the plane of polarised light is considerably greater than that of dextrose, being about +140°, as against +52° for dextrose. Maltose yields an osazone when heated with phenyl-hydrazine hydrochloride. When heated the crystals (phenyl-maltosazone) melt at 206° C., and this, together with the shape of the crystals and their specific solubility in 75 parts of boiling water, renders the identification of maltose easy. Maltose, like cane-sugar, is non-assimilable, for, if injected into the circulation, it is excreted unchanged. Before absorption it has to be converted into dextrose, and this is effected by a ferment, *maltase* (pp. 218, 264 and 296).

Lactose, or milk-sugar, is found solely in milk. It reduces Fehling's solution, and has the same rotatory power as dextrose, but it does not reduce Barfoed's reagent, nor does it undergo direct alcoholic fermentation with yeast. If boiled with dilute mineral acids, it is converted into equal parts of dextrose and galactose. Lactose readily undergoes lactic fermentation, as, for instance, in souring milk. The cause of this is a micro-organism; but there are reasons for believing that an enzyme may also bring it about. In spite of the fact that isolated lactose is unable to ferment in the presence of yeast, yet an alcoholic fermentation is capable of occurring in milk, such, for instance, as in the *koumiss* from mare's milk and *kephir* from cow's milk. It is probable that the changes which bring this about are very complex, and due to several organisms.

Lactose, like sucrose and maltose, is non-assimilable as such, and it is probable that it is changed into dextrose before absorption, not necessarily as the result of the action of any digestive secretion, but during its passage through the intestinal wall. Like maltose, lactose yields an osazone, phenyl-lactosazone, which crystallises in characteristic rounded clumps of yellow crystals. These crystals melt at 200° C., and are soluble in 80 to 90 parts of boiling water.

Monosaccharoses, or Simple Sugars.—A simple sugar may be either an aldehyde or ketone linked to one or more alcohol groups. Such sugars may contain from two to nine carbon atoms, and so are termed bioses, trioses, tetroses, pentoses, hexoses, etc. Of these, the most important are the pentoses ($C_5H_{10}O_5$) and the hexoses ($C_6H_{12}O_6$), the former being widely distributed in plants, the latter occurring in three important forms in the animal organism—glucose, galactose, and fructose. Glucose and galactose are aldo-hexoses, fructose a keto-hexose. The di- and poly-saccharoses furnish on hydrolysis the monosaccharoses, or simple sugars. Of these, the most important one is—

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* A solution of cupric acetate to which acetic acid is added.

Dextrose, Glucose, or Grape-Sugar.—This is probably the form to which all sugars must be reduced in the alimentary canal, whether before or during absorption, in order that they may be assimilable by the tissues. In its ordinary reactions dextrose resembles maltose, but may be easily distinguished from it by the following differences in behaviour. Its specific rotatory power is only +52°. It reduces Barfoed's reagent (see Maltose). The osazone it forms, phenyl-glucosazone, crystallises in fine yellow needles; these melt at 205° C., and, unlike the corresponding compound of maltose, are almost insoluble in water. Dextrose is capable of undergoing three fermentations—*i.e.*, alcoholic, lactic, and butyric; the last two are probably always present in the intestinal canals of animals, especially after a carbohydrate diet. Dextrose is found in the blood and many organs of the body. It is also the form in which sugar escapes by the kidneys in diabetes.

Lævulose (Fructose).—This occurs in fruits and honey mixed with glucose. It may also be prepared by acting upon cane-sugar with sulphuric acid, by which means the cane-sugar is converted into equal parts of dextrose and lævulose.

Pentoses occur in nature either free or in the form of condensation products, gum-like bodies, or celluloses $(C_5H_8O_4)n$, the latter on hydrolysis furnishing the pentoses $(C_5H_{10}O_5)$. Arabinose is derived from the pentosan (araban) of gum arabic. They are obtained also from the decomposition of certain nucleo-proteins, and may occur in the urine. They reduce metallic oxides in alkaline solution, furnish osazones, and are dextro-rotatory or inactive. They are not fermented by yeast.

Tests for Sugar—1. *Trommer's.*—An excess of caustic potash and a small amount of dilute solution of copper sulphate are added to the fluid and the whole heated. The copper is reduced to suboxide by the sugar, and a red precipitate falls. Fehling's solution, which is used as a *quantitative* test for sugar, consists of hydrated cupric oxide in caustic soda, and the double tartrate of sodium and potassium. The principle of this test is the same—viz., the reducing action of the sugar, which robs the cupric compound of its oxygen.

2. *Moore's.*—A solution of sugar boiled with caustic potash turns brown.

3. *Böttcher's.*—Bismuth oxide and excess of caustic potash are added to the fluid containing sugar and heated. The solution becomes grey and then black, from the deposition of metallic bismuth.

4. *Picric Acid Test.*—Boil the solution of sugar with a little picric acid and caustic soda in small quantities; a browd-red opaque coloration is obtained.

5. *Fermentation Test.*—The fluid containing a piece of yeast is placed in a tube and inverted over mercury. If sugar is present it undergoes fermentation, and carbonic acid is given off, which collects in the tube.

The osazone tests have already been described under the respective sugars. They are very important to chemists for the discrimination of the various sugars, as well as for their identification.

The inositols do not belong to the carbohydrates. They constitute a small group of natural compounds which are hydro-aromatic compounds (hexa-oxy-hexa-hydro-benzene). Some are optically active, others inactive. The form which is found in heart muscle is optically inactive. It may be separated in large colourless crystals which, on solution have a sweetish taste, hence the old name applied to this body, ‘muscle sugar.’ It does not reduce Fehling’s solution. Many compounds of this group are met with in plants, quercitol (in acorns), i-inositol (in peas and beans, and in combination with phosphoric acid in the husk of various cereals).

The Ferments.

The conversion of one substance into another by the process of fermentation must have acted as a stimulus in the search for the philosopher’s stone. To the ordinary mind, if sugar could be converted into alcohol, why not lead into gold? The extraordinary phenomenon of a body being wholly changed into another, and bearing not the faintest resemblance to its progenitor, is not only one of the astonishing facts recorded by chemistry, but one of the wonders of science. The name ‘fermentation’ was applied to the oldest example of this phenomenon, and indicated a restlessness or agitation in the fluid, the outcome of the generation of gas. When, later on, this was shown to be due to the activity of micro-organisms, these latter were naturally described as **ferments**. This term has remained, though fermentation is now known not to be exclusively produced by living organisms, but that non-living material may also excite it. To these non-living ferments the distinguishing name of enzymes is applied.

The action of enzymes may be regarded as a catalytic process, in which the velocity of a reaction is increased from the presence of a catalyst. Like most catalytic processes, enzyme reactions are usually reversible—that is to say, whether one starts with the mother substance on which the enzyme acts or with the products of the reaction the same position of equilibrium is finally reached. Inorganic catalysts have not the very specific character of organic enzymes. The enzyme acts upon a special substance (substrate), and on it alone. The conditions under which the reaction takes place—for example, temperature and reaction of medium—influence the velocity of the reaction.

The larger number of enzymatic processes are hydrolytic, as, for example, the diastases, maltase, invertase, pepsin, trypsin, erepsin, arginase, guanase, adenase, lipase, and urease; but there are also oxidising (oxidases) and reducing enzymes (reductases) which undoubtedly play an important part in tissue metabolism (see p. 403).

The reversibility of enzyme actions is a most important property, enabling the enzyme under one set of conditions to produce a decomposition of the mother substance and under other conditions to synthetise the products of decomposition. Thus, lipase may not only break down olein into oleic acid and glycerol, but may also synthetise these bodies to olein. Pepsin, trypsin, and erepsin may also in all probability act reversibly. Throughout the text the various important enzymes have been referred to and the nature of their reactions discussed.

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